



**AN EXPLORATION OF THE EFFECTS OF
GENETIC DRIFT ON THE ENDANGERED
RED-COCKADED WOODPECKER**

THESIS

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AFIT/GEM/ENV/06M-12

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Presented to the Faculty
Department of Systems and Engineering Management
Graduate School of Engineering and Management
Air Force Institute of Technology
Air University
Air Education and Training Command
In Partial Fulfillment of the Requirements for the
Degree of Master of Science in Engineering and Environmental Management

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March 2006

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Abstract

The Red-cockaded Woodpecker (RCW) (*Picoides borealis*) is classified as an endangered species under the Endangered Species Act of 1973. The RCW is endemic to the longleaf pine forests of the southeastern United States. The two main factors contributing to the RCW population declines are the suppression of natural wildfires during the 1900's and the habitat fragmentation due to inappropriate timber harvest techniques. Given the endangerment of the RCW, the genetic variation of the small populations will decrease over time due to random genetic drift. The only method of battling the negative effects of random genetic drift is to move, or translocate, genetically diverse birds into the fragmented populations thereby increasing the genetic diversity of the small populations. The objective of this research effort is to explore the effects of random genetic drift on small RCW populations and to determine the most efficient management strategies to be used in different situations. This research introduces a new concept in the linking of a loss of genetic diversity to a loss of fitness within the RCW population. A model, representing the RCW and their longleaf ecosystem, is simulated across many different environmental scenarios. A study of the model results shows that ecosystem managers need to rethink their methods of managing endangered populations. Instead of focusing on the quality of the physical habitat using land management techniques, the model suggests that when the population is low in numbers, translocation is the only management technique capable of restoring the endangered population.

Acknowledgments

First and foremost, I would like to thank God for providing us with endless research opportunities throughout His creation. I have only scratched the surface of the miracles that are present within thousands of ecosystems around the world. I would like to thank my Lord and Savior Jesus Christ, without whom I am *nothing*. He gave me the strength and perseverance to finish this research effort and He continually reminded me of His encouraging love and saving grace.

I would also like to thank my brother in Christ and faculty advisor, Dr. Michael Shelley. His boundless knowledge and encouraging guidance both on an academic and a spiritual level will remain with me for my entire life. I also owe a great deal of appreciation to my thesis committee members, Dr. Charles Bleckmann and Lt Col Ellen England for their guidance, recommendations, and expertise throughout my efforts.

I am also indebted to Kim Bittle, now the district ranger at Shoal Creek Ranger District in Alabama; Chuck Hess, the District Biologist at the Apalachicola National Forest; and Steve Parrish, the Assistant Fire Management Officer at the Apalachicola NF. These U.S. Forest Service individuals are responsible for managing the largest and one of the few healthy RCW populations in the world. The valuable knowledge they so willingly passed on to me made it possible to model a prescribed burning regime within a longleaf ecosystem.

I am also grateful for the love, support, and endless patience of my wife. Her selfless attitude was the inspiration behind my success at AFIT. I truly could not have done this without her.

Ryan E. Nelson

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I. Introduction

Background

The Department of Defense (DoD) owns and manages approximately 29 million acres of land on about 425 major installations throughout the United States (Boice, July 1996). With these large expanses of land, the DoD has a very important role in the management of habitat for threatened and endangered species. Currently the DoD is responsible for 320 endangered species on 252 separate installations and the Air Force is responsible for more than 70 endangered species known to occur on 45 installations (Boice, Sept 1996). DoD owns and controls the highest known density of endangered species, approximately 220 species, of all federal land (Boice, July 1996). From FY 1991 to FY 2004 the RCW was the endangered species most invested in by the DoD at \$67.4 million (DENIX, 2005). The DoD clearly recognizes the importance of good-stewardship of the environment. However, the DoD's important environmental management responsibility often conflicts with the dynamic missions of DoD installations. During the past decade, approximately 15 military installations have needed to adjust their training missions to avoid further degradation of endangered species habitat (Boice, 1996). When faced with situations that might hurt an endangered population or risk national security, the DoD must weigh the alternatives and chose carefully.

Many issues arise when the population of a species begins to decrease. For example, a small population has a higher rate of inbreeding, which results decreases in

genetic diversity. Also, as a population becomes smaller, a phenomenon known as random genetic drift occurs. Random genetic drift, like inbreeding, causes a decrease in the genetic diversity of the endangered species. Random genetic drift within small populations is well known; however, the effects of random genetic drift are not as well known. Due to the general lack of understanding of the effects of genetic drift on small populations, it is no surprise that those effects are not widely considered in endangered species management practices. Most management practices focus solely on habitat management without considering the health of the species. This research effort addresses this lack of understanding of genetic drift and explores the possible effects of genetic drift on the Red-cockaded woodpecker (RCW) (*Picoides borealis*).

The Red-cockaded woodpecker is listed as an endangered species under the Endangered Species Act of 1973. The endangered classification of the RCW can be primarily attributed to fragmentation of habitat. Early agriculture and logging industries in the southeastern United States around the turn of the 20th century had an enormous impact on the old growth longleaf pine forests, which are essential to the survival of the RCW (USFWS, 2003). Unlike other woodpeckers, the sensitive RCW requires living, longleaf pines to bore out cavities, or living spaces, which can take over 4 years for the bird to complete (Zhang, 2004). Due to the harvesting of old growth, longleaf pines in the US, the distribution of the RCW has become contracted and fragmented (Jackson 1971, 1978; Lennartz et al., 1983b). Fragmentation is a limiting factor to the survival of the RCW (USFWS, 2003).

A key example of RCW management on DoD lands exists on the Poinsett Weapons Range in South Carolina. The Poinsett Weapons Range, operated by Shaw Air

Force Base (SAFB), has approximately 25 RCW's located in 5 active clusters. A cluster is the aggregation of active and inactive RCW cavities within an area (USFWS, 2003). SAFB adheres to the mandated requirements of the Endangered Species Act, DoD Directive 4700.4, *Natural Resource Management Program*; Air Force Instruction 32-7064, *Integrated Natural Resource Management*; and AF Policy Directive 32-70, *Environmental Management* (Schroeder, 2001). Shaw's Red-cockaded Woodpecker Plan identifies the main management concerns for the RCW as breeding success, loss of cavity trees, beetle infestation, understory hardwood control, cavity-invading flying squirrels, and a small population size which leads to random genetic drift and possible elimination of the sub-population (the concept of random genetic drift is the focus of this research, using the RCW as an example endangered species) (Shaw, 1995). SAFB manages their RCW populations by drilling artificial cavities for the birds, replacing harvested timber with pure longleaf pine, prescribed burn rotations, pine stand thinning, and translocation of individual birds (Shaw, 1995).

Problem Statement

Given the population fragmentation, the non-migratory, or sedentary habits, and the slow nesting-building habits of the RCW, the genetic variation of the small populations will decrease over time due to random genetic drift. In the USFWS recovery plan for the RCW (USFWS, 2003), it was recognized that fragmentation of habitat posed a serious threat to the genetic diversity of sub-populations and therefore the entire species (Stangel et al., 1992). D. T. Suzuki et al explain genetic drift very well:

If a population is finite in size (as all populations are) and if a given pair of parents have only a small number of offspring, then even in the absence of all selective forces, the frequency of a gene will not be

exactly reproduced in the next generation because of sampling error. This process of random fluctuation continues generation after generation, with no force pushing the frequency back to its initial state because the population has no "genetic memory" of its state many generations ago. Each generation is an independent event (1989).

In short, Suzuki et al. state that random elimination (e.g. Natural disasters, human intervention, habitat destruction, etc) of genetically unique individuals (e.g. RCW with a longer beak for improved boring into the pines, or a RCW with a stronger immune system) will cause the small population to become homozygotic, or genetically similar. Furthering the problem, fragmented populations are vulnerable to a variety of factors, including catastrophic environmental events, random demographic fluctuations, disease outbreaks, and predators. Small, isolated populations, such as endangered species, are much more susceptible to the loss of genetic diversity (Terborgh & Winter, 1980). Large populations lose genetic variability slowly, and the long term effects of random genetic drift would be offset by mutation, or the occasional migration of RCW in-between sub-populations (Stangel et al., 1992). Mutation is assumed to occur over a long period of time; thus, within the short duration of this model, mutation has no ability to increase genetic diversity. Within large populations, a species will have many more genetically diverse individuals than small populations. This is because the passing of traits from one generation to the next happens in a random manner. Within a small population, there is a higher probability that the traits critical to survival will randomly be eliminated from the population from one generation to the next. Loss of genetic diversity has a negative impact on the species' ability to adapt to its environment. It is important to understand that genetic drift is present at all population levels; however, as the population size decreases, the effects of genetic drift are greatly enhanced.

Purpose of Research

The purpose of this research is to provide a suitable model of the dynamics of genetic diversity within an endangered population in their natural environment. Also, the research explores the relationship between changes in genetic diversity and a species' reaction to that change – a relationship that is very hard to study within nature. The model could then be used by ecosystem managers to foresee reasonable ranges of effects of decreasing genetic variability of a population on the health or survivability of that population and to help design land management strategies to counter this effect.

Research Objectives

Although much research has been performed on genetic variability, few researchers have attempted to quantify genetic variation and predict its long-term effects on the quality of life for small populations. A model of the natural environment will be used to simulate the processes that lead to the degradation of the genetic variability and to uncover the best management practices that can be used to enhance the genetic variability, and thereby the quality of life of the population. The following research objectives will be addressed:

1. Determine the extent to which genetic diversity levels within a small population impact the ability of the species to utilize and exploit its habitat.
2. Determine how the ability (or inability) to utilize its habitat affects population sizes of the endangered population and how that, in turn, affects loss of genetic diversity.
3. Determine the most efficient combinations of management strategies (prescribed burning and translocation) that will give ecosystem managers valuable knowledge on

proper management of endangered populations within the context of the significant effects of genetic drift on such populations.

II. Literature Review

The following literature review summarizes current knowledge of RCW behavior and RCW management techniques, the basis for RCW endangerment, and random genetic drift and its effects on small, fragmented populations. Additionally, this review studies current population-genetics models for comparison to and validation of the proposed model.

Red-Cockaded Woodpecker: Biology

The Red-Cockaded Woodpecker is a territorial bird with an average range of 250 acres (Schroeder, 2001). RCWs average about 7 inches tall with a wingspan of 15 inches (USFWS, 2003). RCWs are black and white with a striped pattern on their back and highly distinguishing white patches on the left and right sides of the head. RCWs are named for the small red feathers on the males located between the top of the head and the white cheek patches that might be exposed when the male is excited (USFWS, 2003). Studies have shown that the RCW's typical diet consists of arthropods, such as roaches, ants, centipedes, spiders, and a variety of insect larvae (Hanula et al., 2000). During non-epidemic southern pine beetle years, RCWs are greatly benefited by foraging around dying, beetle-infested pine that are rich in arthropods (Hooper and Lennartz, 1981). However, during the cyclic epidemic southern pine beetle years, the invasive insect can kill many mature pines, potentially destroying RCW foraging habitat and cavity trees (Schaefer et al., 2004).

RCWs are a cooperative breeding species, which means all members of the species assist in raising the young. The RCW lives in groups consisting of a breeding pair and possibly one to four male helpers (USFWS, 2003), which assist the breeding pair

in rearing the young (Lennartz et al., 1987), territory and nest defense, and cavity excavation (USFWS, 2003). On average, a RCW population will rear approximately 1.4 to 1.7 fledglings per group (breeding pair) (USFWS, 2003). The groups normally occupy territories containing a cluster of one or more cavity trees and adjacent foraging areas (Rudolf et al., 2002). The RCW cavities are only excavated within living pine trees and are typically 30 to 42 feet above ground level (MSL). The RCW is endemic to fire-maintained longleaf pine stands of the southern and southeastern United States (Rudolph et al., 2002). Studies have indicated that due to habitat fragmentation and ecosystem mismanagement in the past, RCW populations, particularly those on federal lands, have declined through the 1980s (Conner and Rudolph, 1989) and the early 1990s despite the protection afforded by the Endangered Species Act of 1973 (USFWS, 2003). A new understanding of population dynamics and new management tools in the 1990s brought with them stabilization and even increases in a small number of RCW populations (USFWS, 2003). However, despite the slight increases in some managed populations, overall RCW population trends are showing consistent decreases in numbers (Jackson, 1991).



Figure 2.1 Adult Male Red-cockaded Woodpecker
(photo taken by Mike Dazenbaker) *Note the tracking bands on the leg*

Red-cockaded Woodpecker: Endangerment

The two main factors which are responsible for the decline of the RCW during the past few decades are the elimination of controlled burning (fire suppression) and the removal of old growth timber. These two highly influential factors are outlined in the following pages.

Fire Suppression

For many years before Europeans first visited North America, the RCW lived in the vast longleaf pine stands where frequent, naturally-occurring fires burned much of the under/midstory within the ecosystem (Conner et al., 2004). The primary means of natural fires was lightning strikes (Ware et al., 1993). Native Americans also used fire as a means of clearing the understory for easier hunting and gathering, and to support

vegetation used for specific purposes (Wickstrom, 1987). For fear of harmful wildfires, by 1924, most state and federal policies called for strict fire suppression and prohibited using controlled fire for forest management purposes (van Wagtendonk, 1995).

Topography, bodies of water, and government agencies were the main agents of fire suppression (Ware et al., 1993). The near complete termination of natural wildfire coupled with inadequate usage of controlled burns to manage forests has led to the severe invasion of dense hardwood understories (Rudolph et al., 2002). Although it has been found that dense hardwood midstory growth has negative impacts on RCW populations, the actual reasons behind the negative impacts are not well understood. Studies show that RCWs in loblolly-shortleaf pine stands, which are indicative of dense hardwood understories, prefer to forage in areas of the forest with significantly less hardwood understory (Rudolph et al., 2002). In addition, studies show that RCWs find a source of calcium in snail shells, which are only exposed to the woodpecker after the groundcover is burned (Hanula et al., 2000). Because of a now well-established hardwood understory due to fire suppression, more intense fires coupled with herbicide treatment may be necessary for treatment in many areas with the developed understory (Provencher et al., 2001).

Harvest of Old Growth Timber

RCWs are highly sensitive to nearly every aspect of the environment around them. RCWs require living, medium to large-sized tracts of mature pine to bore cavities into and maintain healthy population numbers. The RCWs typically excavate cavities in living southern pine trees, including shortleaf, loblolly, longleaf, and other less common species of pine (Hooper et al., 1991). However, when available, old growth longleaf pine

is favored over the other pine species (Ross et al., 1997). Nest productivity of RCW in longleaf forests is greater than in shortleaf or loblolly pine forests (Schaefer et al., 2004). The ability of the longleaf pine to produce large amounts of resin, or sap, is very important to the RCW. The RCW will bore a cavity into the dead heartwood of the mature pine. During and after the cavity construction, the RCW will peck small holes called "resin wells" around the main entrance hole to the cavity, often extending 4 or more feet above and below the cavity entrance hole (USFWS, 2003). The resin wells, which are kept open by RCWs, exude large amounts of sap. The RCW will keep the sap from clogging the entrance while leaving enough sap to form a much needed barrier to deter predators such as climbing snakes (Conner et al., 2004). As the only species to regularly bore into living pine, the RCW is also considered a keystone species in pine ecosystems by providing shelter for secondary dwellers when the cavity is abandoned by the RCW (Conner et al., 2004).

Southern pine is the most important commercial timber species in the southern United States (Zhang, 2004). Once harvested, the old-growth longleaf pine is generally replaced by the faster growing southern pine, such as loblolly pine or shortleaf pine. The new-growth pine is then harvested before they become mature enough for the RCW to excavate a cavity. The steadily declining acreage of mature pine stands due to timber harvests has lead to severe fragmentation (Cox and Engstrom, 2001) within RCW populations. Ligon et al. suggested that the timber industry can continue, but large clear cuts, and harvests of old growth pine stands must be avoided (1991). The answer lies in selective thinning, or harvesting portions of the medium sized pine and leaving the old-growth and a portion of the medium-growth trees to replenish the old-growth as they die.

Again, the RCW prefer the longleaf pine, however, other pine species are frequently excavated by the bird. The four species of pine that are typically utilized by the RCW include longleaf pine (*Pinus palustris* Mill.), loblolly pine (*Pinus taeda* L.), shortleaf pine (*Pinus echinata* Mill.) (Hooper et al., 1991), and slash pine (*Pinus elliottii* Engelm.) (Bowman, 1999; Ross et al., 1997). The following presents a biological and physiological description of each species typically utilized by the RCW:

Longleaf Pine (*Pinus palustris* Mill.)

Prior to European colonization coastal plain forest ecosystems in the southeastern U.S. were dominated by longleaf pine stands with open understories (Michigan Tech University, 2003). Historically, the large tracts of longleaf pine are estimated to have covered between 60 million acres (Boyer, 1990) and 90 million acres (Michigan Tech University, 2003). Longleaf pine once occurred along the south Atlantic coast, around the Gulf Coastal plains, and north through the Appalachian foothills of Northern Alabama (Harlow and Harrar, 1941). Today, approximately 4 million acres of severely fragmented longleaf pine stands exist in the southeastern U.S. (Boyer, 1990). Longleaf pine ecosystems are considered threatened ecosystems in North America; less than 2% of the Coastal Plain is dominated by the longleaf pine (Michigan Tech University, 2003).



Figure 2.2 Longleaf pine/wiregrass communities. Note the park like appearance of the stand (photo from www.conservationsoutheast.com, photographer unknown)

Longleaf pine is very tolerant of fire (Coggin, 2002). Because of this fire tolerance, natural longleaf pine stands are open, meadow-like forests with groundcover associated with the frequent burning (Boyer, 1990). The openness of the virgin longleaf stands allow large amounts of sunlight to reach the forest floor which stimulates the growth of vegetation and a foraging ground for many wild animals (Coggin, 2002). Mature longleaf pine is capable of reaching 80 to 125 feet in height and 30 to 40 feet of canopy spread (Gilman and Watson, 1993). Longleaf pine needles vary from 8 to 18 inches in length in 3 needle clusters (Symonds, 1958), or fascicles. A weeping variety with needles up to 24 inches in length has been recorded in North Carolina (Harlow and Harrar, 1941). Longleaf pine reaches full maturity in approximately 150 years and will achieve a seemingly invincible resistance to fire by 25 years of age (Harlow and Harrar,

1941). Longleaf pine grows in warm, humid climates characterized by hot summers and mild winters, preferring temperature averages ranging from 60 to 74 degrees Fahrenheit and annual rainfall from 43 to 69 inches (Boyer, 1990). Longleaf pine prefers well-drained sandy soils (Harlow and Harrar, 1941), but is tolerant of clay, sand, loam, acidic, or slightly alkaline soils (Gilman and Watson, 1993).

Like all pine, longleaf pine is monoecious, meaning that one tree possesses both male and female organs (Boyer, 1990). The respective male and female parts, or strobili, do not favor the same weather conditions, which causes male and female flowers to appear during different time periods, adding complexity to seed development (Boyer, 1990). The growth of the male strobili, also called catkins, is favored during high rainfall throughout the growing season; however, the female strobili, also called conelets, favor wet springs and dry summers (Boyer, 1990). The periods of catkin and conelet production must coincide to successfully reproduce pinecones (Boyer, 1990). Longleaf pine begins producing pinecones from 20 to 30 years of age (Michigan Tech University, 2003). The pinecone may contain 15 to 50 seeds (Boyer, 1990). After reaching maturity, the pinecone will open, dispersing winged seeds that are carried by the wind. After the wind disperses the seeds, a taproot will immediately begin to grow and begin to get a strong foothold in the soil (Harlow and Harrar, 1941). The longleaf seedlings look like small tufts of grass and they may remain this way for 5 to 7 years (National Oceanic and Atmospheric Administration (NOAA) webpage). During the "grass tuft" stage, longleaf seedlings are surprisingly resistant to fire suppression (Boyer, 1990). This is because the growth clusters, or buds, are not exposed during the grass stage. The growth buds do not appear until the tree reaches the sapling stage. The buds are a silver color during the

winter (Gilman and Watson, 1993). The buds, although somewhat heat resistant, are vulnerable to fire (Harlow and Harrar, 1941) and thus the longleaf pine sapling should not be exposed to fire until it reaches approximately 6 feet in height (Coggin, 2002). In comparison to other southern pines, longleaf pine is highly resistant to most diseases, including fusiform rust (Gilman and Watson, 1993), and is an easily managed pine species (Boyer, 1990). Even the destructive southern pine beetle (*Dendroctonus frontalis* Zimmermann), a common pine killer in the southeastern U.S., does not inflict much damage to longleaf pine.

Shortleaf Pine (*Pinus echinata* Mill.)

Shortleaf pine has the widest range of any southern pine in the southeastern U.S. (Lawson, 1990). Shortleaf pine covers over 281 million acres across 22 states (Lawson, 1990) ranging from Long Island, New York along the Atlantic Coast to northern Florida and west to Oklahoma (Sargent, 1965). Second only to loblolly pine in value (Hough, 1963), shortleaf pine is commercially harvested for saw timber and pulp wood (Harlow et al., 1996).



Figure 2.3 A recently thinned shortleaf pine stand (photo taken by Robert Wittwer)

Shortleaf pine prefers well-drained, sandy soils with very low calcium content (Vidakovik, 1991). Shortleaf pine is highly intolerant to shade (Larson, 1990) and although they do not grow well when stressed (e.g. during a drought), shortleaf pine shows a dramatic increase in growth rate when the suppression is released, surpassing even the longleaf in this respect (Harlow et al., 1979). Shortleaf pine prefers humid areas, but is more tolerant to temperature and moisture changes than other southern pines (Lawson, 1990). Generally, shortleaf pine prefers 45 to 55 inches of annual rainfall and the trees cannot withstand areas with an average annual temperature less than 50 degrees Fahrenheit (Lawson, 1990). Shortleaf pine may reach 120 feet tall but normally are in the range of 80 to 100 feet tall (Sargent, 1965). Shortleaf pine needles are generally 3 to 5 inches long in bunches of 2 or 3 needles per fascicle (Harlow and Harrar, 1941).

Like all pines, the shortleaf pine is monoecious (Boyer, 1990), with the male flowers in small, purple clusters and the female flowers in pale red clusters of 2 to 3 on ascending limbs (Sargent, 1965). Once fertilization takes place, pinecones will not develop until the end of the third growing season (Lawson, 1990). Although some abnormal cases exist, shortleaf pine does not bear seeds until 20 years of age (Lawson, 1990). Generally, the pinecones are 1.5 to 2.5 inches in length, 1 to 2 inches in diameter, and are ovoid or conical in shape (Vidakovic, 1991). During the first few years, shortleaf pine seedlings show little growth above ground as the root system becomes more established below ground level (Lawson, 1990). Shortleaf pines rooted in good soil and climate conditions may achieve 60 feet in height at 35 years of age and those 60 years of age may reach 80 feet in height (Harlow et al., 1979). Shortleaf pine reaches maturity at the age of 170 years and, in some cases, may reach an age of 400 years (Harlow and Harrar, 1941).

Like the longleaf pine, shortleaf pines are highly resistant to the damaging fusiform rust (Harlow et al., 1996). However, unlike the longleaf, the shortleaf pine is a normal target of the invasive southern pine beetle during the periodic invasions of the insect (Harlow et al., 1996). Insects such as the Nantucket pine tip moth (*Rhyacionia frustrana*), the redheaded pine sawfly (*Neodiprion lecontei*), and the Pales weevil (*Hylobius pales*) are just a few that readily attack shortleaf pine stands (Lawson, 1990). In general, shortleaf pine is resistant to fires, but seedling crops can be destroyed by fire (Lawson, 1990). By the age of 8 to 10 years, shortleaf pines have the ability to sprout after their main trunks have been destroyed by fire or harvesting (Harlow and Harrar, 1941), giving the shortleaf pine a notable advantage over other pine species.

Loblolly Pine (*Pinus taeda* L.)

Loblolly pine ranges from southern New Jersey along the Atlantic Coastal Plain to central Florida and west to Arkansas and southwestern Oklahoma (Carey, 1992 (2)), covering more than 11.5 million acres (Baker and Langdon, 1990). Loblolly pine is primarily a lowland tree, typically not occurring over 1500 feet in elevation (Sargent, 1965). Loblolly pine reaches 90 to 110 feet in height and 24 to 30 inches in diameter at maturity (Carey, 1992 (2)). Loblolly needles typically are 6 to 9 inches in fascicles of 2 or 3 (Harlow and Harrar, 1941). Loblolly pine prefers climates of hot summers and mild winters with average annual temperatures ranging from 55 to 75 degrees Fahrenheit (Baker and Langdon, 1990). Loblolly pine grows best on soils that have a deep surface layer, high moisture content, and those that are well-drained (Harlow et al., 1979). However, loblolly pine is suited to grow on many different soil types, wet or dry, and therefore is often associated with hardwoods (Harlow et al., 1996). Species commonly associated with loblolly pine include southern red oak (*Quercus falcate*), white oak (*Q. alba*), water oak (*Q. nigra*), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), and southern magnolia (*Magnolia grandiflora*) (Carey, 1992 (2)). The roots of loblolly pine will normally grow laterally much wider than their crown and thus are very effective at preventing soil erosion (Baker and Langdon, 1990).



Figure 2.4 Loblolly pines (photo from <http://www.uafortsmith.edu/Arboretum/LoblollyPine-604>, photographer unknown)

Because it readily grows on many different soil types, loblolly pine is the leading species in the commercial timber industry in the southern U.S., where it makes up greater than half the total pine volume (Baker and Langdon, 1990). However, loblolly wood is not as dense as the other southern pines, causing the wood to be less durable (Hough, 1963). Loblolly pine is monoecious and seed production varies greatly from year to year and is highly dependent on the area climate (Baker and Langdon, 1990). The male flowers occur in tight clusters of yellow spikes and the female flowers, also yellow in color, grow in solitary or clustered groups growing below the apex of the growing shoot (Sargent, 1965). Although pinecone production may begin earlier, regenerative seed production begins at the age of 25 (Baker and Langdon, 1990). The pinecones are typically 2½ to 6 inches in length, reddish brown, and ripen in September and October

(Vidakovic, 1991). Loblolly pine is a remarkably fast-growing tree species. During the first 10 years, loblolly seedlings frequently show growth rates ranging from 3 to 4 feet and ½ to 1 inch in diameter annually (Harlow and Harrar, 1941).

Slash Pine (*Pinus elliottii* Engelm.)

Of the four major southern pines, slash pine has the smallest range which includes much of Florida, north through the lower Atlantic Coastal Plain to South Carolina and west to Louisiana (Lohrey and Kossuth, 1990). Slash pine is typically 80 to 90 feet in height, but is capable of reaching heights up to 120 feet (Harlow and Harrar, 1941).

Slash pine favor warm, wet summers and drier falls and springs with a preferred annual rainfall range of 50 inches per year with the majority falling during the summer months (Lohrey and Kossuth, 1990). Slash pine is typically found growing in sandy soils that are abundant in moisture (Vidakovic, 1991). Within slash pine stands, longleaf pines often inhabit the drier knolls and hills. This distribution is almost certainly from the slash pine's higher susceptibility to fire and the longleaf pine's ability to cope with fire (Harlow et al., 1996). As with all southern pines, temperature seems to be a limiting growth factor for slash pine. Slash pine grows well in areas with an average annual temperature around 63 degrees Fahrenheit, with extremes of 0 and 106 degrees Fahrenheit (Lohrey and Kossuth, 1990). High growth rates and the ability to produce many seeds in a short time are the slash pine's keys to success. Like loblolly pine, slash pine saplings will grow 8 to 16 inches in the first growing season and will achieve 3½ feet per year for their first 10 years (Harlow et al., 1979). Slash pines begin producing seeds at the early age of 20 years (Harlow et al., 1979). Although somewhat intolerant, slash pine is more capable of withstanding competition than longleaf, and less capable than

loblolly (Harlow and Harrar, 1941). Slash pine is known to invade and overtake longleaf stands where fire has been absent for 5 to 6 years (Carey, 1992 (1)).



Figure 2.5 Slash Pine (photo from the Auburn University Horticulture Department - <http://www.ag.auburn.edu/hort/landscape/dbpages/68.html>)

Flowering stages of the monoecious slash pine begin at a relatively early age, usually ranging from 10 to 15 years of age, but occasionally as early as 3 years (Lohrey and Kossuth, 1990). The flowers bloom in January or February (Vidakovic, 1991) and have the appearance of new leaves (Sargent, 1965). The male flowers occur in short dense clusters, which are dark purple in color; the female flowers, also dark purple, occur in pairs just below the apex of the lengthening shoot (Sargent, 1965). The ovoid or

conical-shaped pinecones are normally 3 to 6 inches in length with ridged seeds approximately ¼ inch in length (Harlow et al., 1979).

Slash pine is an important commercial species due to its density and strength (Carey, 1992 (1)). A threat to the health and merchantability of slash is fusiform rust. The disease kills trees and causes deformities often lowering the high market value of the species (Lohrey and Kossuth, 1990). Other problems important to slash pine include root rot, pitch kankers, black turpentine beetles (*Dendroctonus terebrans*) and burning (young trees only) (Carey, 1992). Notably, slash pine is not susceptible to the invasive southern pine beetle (Lohrey and Kossuth, 1990).

Red-Cockaded Woodpecker: Management Techniques

Translocation

In relation to genetic variation, only two mechanisms provide populations with a source of genetic diversity; they are mutation (Lande, 1995) and migration (Lande, 1988). (The term translocation, or human assisted migration, will be used in this study to represent all forms of immigration or migration of bird into an already existing population.) In small, fragmented populations (<500) mutation is negligible (Lande, 1995) and thus translocation of individuals from a larger metapopulation becomes the only mechanism that increases genetic diversity. Individuals introduced into a population by translocation restore alleles that no longer exist in the small population (Lacy, 1987). Translocation becomes the only mechanism that is easily controlled by ecosystem managers (Lacy, 1987). Genetic variation and translocation are discussed in later sections of this chapter.

Artificial Cavities

The RCW is the only woodpecker to excavate its nest and roost cavities in living trees (USFWS, 1999). The excavation process could take several years to complete, and therefore cavity abundance is a limiting resource in RCW habitat (Baggett, 1999).

Although considered a short-term management technique only (USFWS, 2003), the construction of artificial cavities has proven to stabilize or increase otherwise declining RCW populations (Copeyon et al., 1991). Artificial cavity creation symbolizes the first management tool proven to induce the formation of new RCW groups (Copeyon et al., 1991). The use of artificial cavities can help prevent further RCW population declines and can support RCW populations during the next 20 to 30 years while southeastern forests return to the RCW supporting ecosystems that they once were (USGS, 2004).

The two basic types of RCW artificial cavities are insert cavities (Allen, 1991) and drilled cavities (Copeyon, 1990). The drilled cavity type can be further divided into three sub-types: the Copeyon-drilled cavity, the modified drilled cavity, and the Copeyon-drilled start. Both the Copeyon-drilled cavity (Figure 2.6) and the modified drilled cavity consist of an entrance hole for the bird and an access hole for the drill operator to bore out the cavity chamber (USFWS, 2003). The only difference between the Copeyon-drilled cavity and the modified drilled cavity is that the modified uses a larger drill bit for easier construction of the cavity chamber (USFWS, 2003). The Copeyon-drilled start (Figure 2.7) consists of an entrance hole with no cavity chamber. The entrance hole is bored out with the drill bit, thus giving the RCW enough room to finish the cavity (USFWS, 2003). This method saves the RCW vital time during its excavation process.

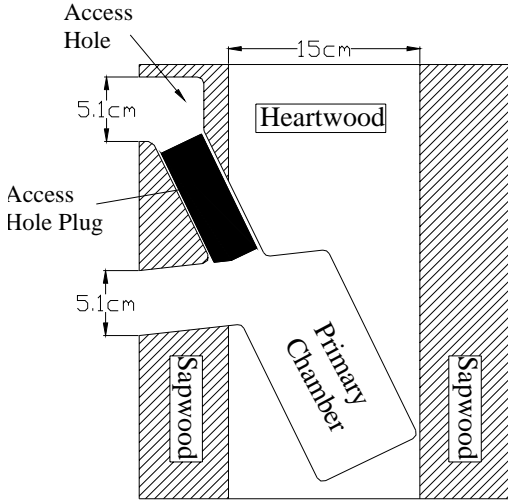


Figure 2.6 Copeyon-Drilled Cavity

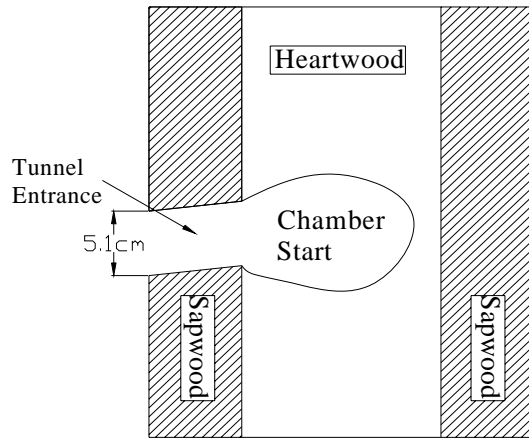


Figure 2.7 Copeyon-Drilled Start

The insert cavity is another type of artificial cavity that is commonly used. Construction of the artificial cavity involves cutting a hole 4 inches wide, 10 inches high, and approximately 6 inches deep into a living pine with a cavity high diameter of no less than 15 inches (Allen, 1991). A wooden box, cut to very specific dimensions is placed into the hole in the living pine. A diagram of the wooden box is shown in Figure 2.8.

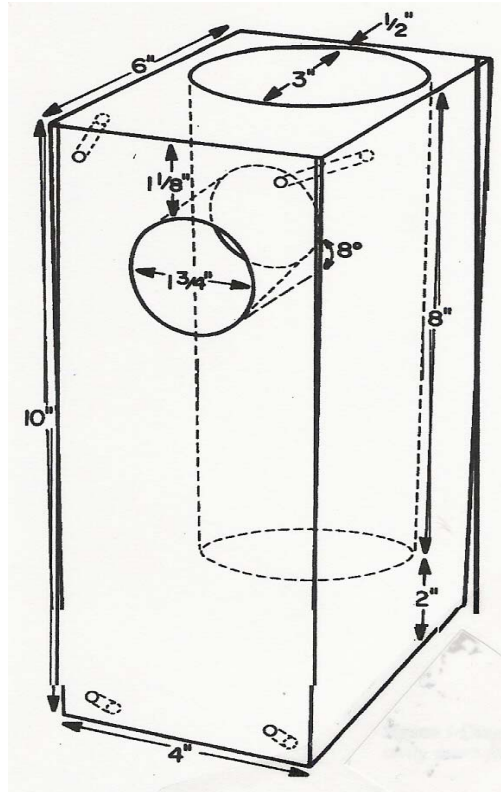


Figure 2.8 Artificial Insert Cavities (Allen 1991)

One problem with the wooden insert artificial cavity, that is also a problem with all cavity types, is that examination of the birds within the cavities requires the use of a light and mirror (Edwards et al., 1997). Studies involving fledglings and eggs are extremely difficult due to hazards involved with the extraction of the fledglings and eggs from the cavity (Allen, 1991). Edwards et al., (1997) offered a solution to this problem by adding a simple access hole under the entrance hole affording researchers hands-on access to the nest within the primary cavity (Edwards et al., 1997). When not in use, the access hole is covered by a wooden plug that screws onto the tree (Edwards et al., 1997). Another problem that seems to occur with the all cavities is deterioration around the cavity entrance due to RCW and other species pecking at the insert box wood around the entrance hole. This problem is solved with the use of cavity restrictor plates. Restrictor

plates reinforce existing cavity entrance holes by surrounding the deteriorating wood around the hole with a thin metal pane that inhibits cavity enlargement (Saenz et al., 2002).

Prescribed Burning

In earlier sections of this chapter, fire suppression is cited as a leading cause of the decline in RCW numbers. Again, the suppression of controlled and natural fires within the vast pine forests of the southeastern U.S. have lead to the dense understory and mixed-species pine stands that are not favorable habitat for the RCW (Rudolph et al., 2002). The solution to this fire suppression problem is prescribed burning. Prescribed burning is essential for the survival of the RCW; however, to be effective, managers must adhere to proper prescribed burning techniques.



Figure 2.9 Prescribed burn in a young pine stand (from the Georgia Forestry Commission website at <http://www.gfc.state.ga.us/Services/FireRelated/PrescribedBurning.cfm>)

There are four main types of prescribed fires: backing fires, head fires, flank fires and spot fires (West, 2005). Backing fires are set to burn against the wind causing this method to be the slowest, and therefore safest, method of prescribed burning (West, 2005). Backing fires burn hotter at the ground surface and do a better job of consuming the dense underbrush (Higgins et al., 1989), which is advantageous to the RCW. Studies have shown that backing fires kill very few pine saplings with ground level stem diameters over 1.5 inches (Lloyd, 1996). Headfires are set to burn in the same direction as the wind, making this method the fastest yet most dangerous method of prescribed burning (West, 2005). Headfires have a lower temperature at ground level than backing fires (Higgins, 1989), but the flames are taller and are capable of killing even larger pines (West, 2005). Flankfires are set by individuals walking abreast (approximately 30 to 50 feet apart) into the wind, setting the fire as they walk (West, 2005). The flames then burn at an angle with the wind. Lastly, spot fires are set at predetermined points within an area and simply burn in outward circles until the fires join (West, 2005).

As previously stated, RCW population declines have stemmed from the decline of native longleaf pine stands and the absence of fire leading to an increase of sub-optimal habitat due to hardwood understory invasion. Given these factors and the sedentary habits of the RCW, the genetic variation of the species will decrease over time due to random genetic drift (USFWS, 2003). The following section discusses the genetic factors in detail.

Genetic Considerations

The two genetic concerns to population dynamics include inbreeding and random genetic drift (USFWS, 2003). In many species, family lines dominated by continual

brother-sister mating or self fertilization tend to become barren after a few generations (Lande, 1988). Inbreeding threatens populations by inserting an immediate lower limit on the population size that is associated with the survival of the species (Franklin, 1980). The lower limit that will remain unaffected by inbreeding, according to Franklin, is approximately 50 individuals (1980). Inbreeding within RCW populations caused reductions in hatching rates and reductions in fledglings that survive to one year old (USFWS, 2003). However, in endangered populations, inbred offspring may not have a lower fitness level than non-inbred offspring; rather *all* the individuals may have a lower fitness level due to random genetic drift (Hedrick and Kalinowski, 2000).

Genetic drift is the loss of genetic variation over time (Yates, 2003). Specifically, genetic drift is the complete fixation of certain alleles, or the elimination of all allele variations at a gene locus, within a population due to the lack of breeding of those individuals that possess the alleles (Franklin, 1980). The transfer of gene variations, or alleles, from one generation to the next is completely random, therefore the movement (or drift) of these alleles after many generations will be very different with no mechanism pushing the alleles back to the initial state. In small populations, random genetic drift is enhanced, causing the small population to lose heterozygosity more quickly and thereby become less able to adapt to changes in the environment (Stangel, 1992). Genetic drift is more sensitive to the population size than inbreeding. Whereas 50 individuals is the minimum number to counter the effects of inbreeding, 500 individuals is the critical number to counter the effects of genetic drift within a population (Lande, 1988).

The genetic variation of small fragmented populations often poses a serious threat to the survival of that population. To avoid the detrimental effects of genetic drift and

eventual extinction, small, fragmented populations may benefit from the introduction of new, genetically diverse individuals from an outside population (Hedrick and Kalinowski, 2000). The RCW is sedentary and therefore natural migration between fragmented subpopulations is unusual, thus translocation is often the answer. Translocation of 1 to 10 migrants per generation can reverse the effects of genetic drift and sustain the genetic variation of the population (Mills and Allendorf, 1996).

Various models exist that examine extinction. However, most of these models examine large collections of species using statistics and probabilities based on past data, ignoring the specifics of the species (like ecology and population structure), and therefore cannot accurately predict the extinction of a particular species (Lande, 1988). Modern endangered species management has a general lack of information and knowledge on the patterns of genetic variation and diversity *within* the species (Lacy and Lindenmayer, 1994). The effects of population size on genetic diversity have been studied, however, little is known about the effects of genetic diversity on the overall health of a population. A longitudinal, deterministic model, with the ability to predict genetic diversity and population sizes based on various parameters throughout time, is needed. It is important to note that any model, especially one dealing with nature, is an oversimplification or an abstract of the true natural situation (Crow and Kimura, 1970). The models that simulate the dynamics of population genetics are mathematical (Crow and Kimura, 1970). The mathematics involved in our model are described in the following paragraphs.

The effects of population size on genetic diversity due to genetic drift are quantified in empirical formulas from previous research. According to Lande, the effects

of population size on genetic variation can be quantified by the following equation (1995):

$$\text{Equation 2.1: } \frac{d\bar{V}_g}{dt} = -\frac{\bar{V}_g}{2N_e} + V_M$$

Where \bar{V}_g is the average variance across the gene pool of the managed population, t is time in generations, N_e is the effective population size, and V_M is the genetic variance gained from mutation (Lande, 1995). Except for translocation, the only avenue for increasing genetic variance in a population is mutation. The effects of mutation on genetic diversity are highly debated among researchers; therefore those effects are not included within this model. Thus, the Lande equation can be simplified as follows:

$$\text{Equation 2.2: } \frac{d\bar{V}_g}{dt} = -\frac{\bar{V}_g}{2N_e}$$

Equation 2.2 shows genetic diversity as a function of the initial amount of genetic diversity and the population size. The change in diversity, shown mathematically by Lande's equation, is a result of random genetic drift. Additional terms showing the change in genetic diversity due to translocation can be added to Equation 2.2. According to Lande, the effects of translocation and random genetic drift on genetic variation within a small population can be modeled by the following equation (1995):

$$\text{Equation 2.3: } \frac{d\bar{V}_g}{dt} = -\frac{\bar{V}_g}{2N_e} + m(\bar{V}_g(0) - \bar{V}_g) + \frac{m(1-m)}{2} * \bar{V}_z$$

Where m is the immigration rate or the proportion of the translocated individuals within the fragmented population; the immigration rate, m , equals the number of individuals translocated divided by the fragmented effective size, N_e (Yates, 2003). $V_g(0)$ (bar) is the additive genetic variance from the translocated individual with the mean phenotype (Lande, 1995). The phenotype is the “genetically determined physical appearance of an organism, as considered with respect to all possible genetically influenced expressions of one specific character (definition of phenotype; Webster’s Dictionary, 1988). The statistical variance in the probability distribution of the mean phenotype within the managed population is V_z (Lande, 1995). The change in this statistical variance caused by translocation is expressed as follows:

Equation 2.4:
$$\frac{d\bar{V}_z}{dt} = -2m * \bar{V}_z + \bar{V}_g * N_e$$

In the book, “*An Introduction to Population Genetics Theory*,” F. J. Crow and M. Kimura modeled heterozygosity within animal populations contrived of sexually reproducing males and females (1970). Like Lande, Crow and Kimura are mathematically deriving the effects of population size on genetic diversity due to random genetic drift. Crow and Kimura’s equations, which are mechanically different from Lande’s equations, generate very similar genetic diversity levels, giving further validation to the Lande equations. Crow and Kimura’s equation is as follows:

Equation 2.5:
$$H_t = \left(\frac{N-1}{N} \right) * H_{(t-1)} + \left(\frac{1}{2N} \right) * H_{(t-2)}$$

Where H_t is the heterozygosity at time t , and N is the effective population size.

The genetic diversity remaining given by each of the equations 2.2 and 2.5 is shown in Figure 2.10.

Table 2.1 Validity check. Note the similarity between the two outputs of the mechanically different equations.

time (generations)	Population	Diversity remaining (Crow/ Kimura)	Diversity remaining (Lande)
0	500	1	1
300	500	0.74092876	0.74081822
600	500	0.54897597	0.54881164
900	500	0.40675249	0.40656966
1200	500	0.30137492	0.30119421
1500	500	0.22329757	0.22313016
1900	500	0.14971082	0.14956862

Lande's equation, as simplified in equation 2.3, provides an accurate mathematical basis for a model of the effects of genetic drift on small, fragmented RCW populations. The concepts behind this model are described in detail in chapter 3.

III. Methodology

Ecosystem managers have the enormous responsibility for managing their complex natural systems while also ensuring that their ecosystem is sustained for future generations. Certain ecosystems are more fragile than others, especially those ecosystems that inhabit endangered species. Decisions made by the ecosystem manager must be made with extra caution when dealing with endangered species. Small habitat changes have the potential to bring extinction to the fragile species. Models forecasting the dynamics of endangered species and their ecosystems can help ecosystem managers balance their fragile ecosystems by making better decisions.

Model Conceptualization

Before modeling the life cycle and genetic considerations of the RCW, one must lay the ground work by modeling the RCW habitat. It is known that the quality of the habitat in the longleaf pine ecosystems of the southeastern United States greatly affects the health and viability of RCW populations. The RCW requires adequate habitat to survive therefore it is important to accurately simulate the RCW habitat within the model. In this model, the habitat is considered to be the RCW cavity tree, the area immediately adjacent to the cavity tree, and the foraging, or feeding range (85 hectares). The habitat is made up of two sections within the model, a longleaf pine section and an encroaching hardwood section that must be kept at bay using prescribed burns.

Longleaf Pine Modeling

The longleaf section of the model simulates the life cycle of a longleaf pine. The life cycle is divided into 6 age classes: grass stage, sapling, small pole, large pole, mature, and old growth. Each age class has its own mortality based on an ecosystem resource

carrying capacity. The carrying capacity is required to give the longleaf pine a logistic growth curve, which is indicative of natural populations. The carrying capacity is assumed to be the average number of longleaf trees that can survive on the 85 hectare RCW foraging area. This capacity is assumed to be 22,920 longleaf trees per 85 ha (all age classes, sapling through old growth). This number is based on the assumption that each tree (sapling through old growth) requires an average of 1 yard radius distance from other trees to grow successfully. Based on this 1 yard radius assumption, an 85 ha area can sustain an average of 22,920 longleaf pines. At each point in time within the simulation, the model distributes the carrying capacity in the system to each longleaf age class equally.

Also, each longleaf age class is affected by prescribed burning, especially when the burn is very intense. It is assumed that the maximum fire intensity which any longleaf can withstand is 7000 KW/meter (this is discussed in the prescribed burn section). The effect of fire on each age class is very different, so different graphical relationships represent the fire effect for each age class. For example, the grass stage longleaf pine can surprisingly withstand a moderately intense fire (Boyer, 1990). However, after the growth buds emerge in the sapling stage, the tree is considerably more susceptible to fire (Harlow and Harrar, 1941). As the trees age after the sapling stage, they become more and more resistant to fire. Again, the relationships between the age classes and the number of trees lost to fire are explicitly formulated in the model.

Also affecting each age class is the aging up of trees from one age class to the next. As this information is not readily available, an assumption must be made. Since some age classes contain more trees than other age classes (i.e. grass stage – 1 to 5 year

old trees, large pole – 16 to 30 year old trees, etc), the most logical method of aging trees to the next class is to assume that one year group is aging up to the next class while the younger trees remain in that age class. For instance, since there are trees ranging from 1 to 5 years of age in the grass stage, those trees that are 5 years old should be the ones to age up. Assuming that the trees within each age class are evenly distributed, 1 tree out of every 5 trees will age up, and so the first order age up coefficient for the grass stage is $1/5$ or 0.2. For the large pole, the age up coefficient is $1/15$ or 0.067. This methodology is applied over all the age classes.

Longleaf regeneration is also an important aspect in modeling the longleaf ecosystem. The complex regeneration process is considered to be a function of five variables. These variables are as follows: 1) the number of longleaf seed trees, or cone-bearing trees; 2) the number of successfully germinated longleaf seeds per tree; 3) the amount of sunlight penetrating to the forest floor; 4) the hardwood understory density (choking effect); and 5) the amount of litter, or non decomposed biotic material present on the forest floor.

The number of longleaf seed trees is the number of trees within the small pole through old growth age classes (trees old enough to bear pine cones). This number is multiplied by the number of seeds germinated per tree, which is assumed to be 15 seeds per tree (Boyer, 1990), to get the number of germinated seeds within the 85 hectare range. The remaining factors range from 0 to 1 - 0 being the worst and 1 being the best. The number of germinated seeds in the range is multiplied by each factor. The factors are described in the following paragraph.

The sunlight penetration fraction is based on the density of adult trees. It is assumed that a tree density of 1000 adult trees (small pole through old growth) per 85 hectares would let no sunlight penetrate to the forest floor, resulting in a no-regeneration scenario. As longleaf adult tree density increases, the fraction of sunlight penetrating decreases, thereby causing a decrease in longleaf regeneration. Also, the hardwood understory can easily overrun a pine forest that is fire suppressed. Increased hardwood density greatly inhibits the regeneration of longleaf and can only be prevented by a frequent prescribed burn cycle (Rudolph et al., 2002). Lastly, the amount of litter on the forest floor can block the seeds from reaching the nutrient-rich seed bed. Like the hardwood understory encroachment, the amount of litter can only be controlled by prescribed burning. This relationship will be discussed in more detail in the prescribed burning section.

Prescribed Burn Modeling

The prescribed burn section of the model simulates an 85 hectare controlled burn at a frequency preset by the modeler. It is assumed that each burn is performed in ideal weather and wind conditions. Within the model, the amount of fuel, or litter on the ground determines the intensity of the burn. For example, if the pine stand has not been burned in 10 years, the fuel built up over the 10 year period will burn very intense. With the 10 year burn cycle, increased longleaf mortality rates, especially at the younger age classes, are highly likely. In contrast, a more frequent 3 year burn cycle closely resembles the original natural fire regime that was the lifeblood of the longleaf pine ecosystem. The 3 year burn is much less intense simply because the amount of fire fuel on the ground accounts for only 3 years worth of litter, assuming that all the fuel is

burned during each burn. Fire suppression, or the no-burn alternative, within the model will allow for a quick invasion of a hardwood understory, choking out the foraging ground of the RCW and bringing them to extinction in as little as 75 years – a frighteningly accurate description of the current state of the RCW.

To accurately model the fuel, or litter, on the ground the sources of the fuel must first be modeled. Fuel is a function of basal area. The basal area of a tree is the cross-sectional area approximately 4.5 feet from the ground. Within the model, an average cross sectional area for each tree age class is assumed: sapling – 0.022 sf (2” diameter), small pole – 0.2 sf (6” diameter), large pole – 0.79 sf (12” diameter), mature – 1.8 sf (18” diameter), and old growth – 2.4 sf (21” diameter). The average basal area for each age class is then multiplied by the number of trees in its respective age class to get each class’s basal area. The sum of all age classes’ basal areas is the total longleaf basal for the 85 ha range. The basal area, along with the number of years since the last burn, is then used to determine an amount of fuel on the ground. The fuel consists mostly of a pine needle layer with fallen tree branches. This layer will accumulate until decomposition equilibrium is reached. As the fuel layer deepens, the layer that is decomposing also deepens until the amount of fuel falling onto the ground equals the amount of fuel decomposing. According to data from the US Forest Service, litter accumulations will reach a steady-state at the 20 year point. The following chart shows the USFS data:

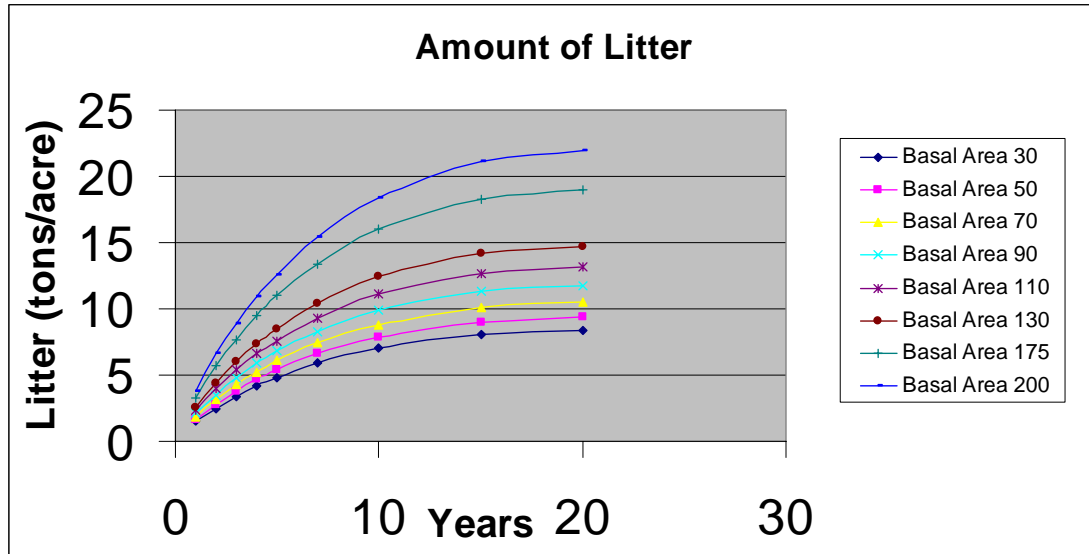


Figure 3.1 Litter amount for various basal areas over a 20 year period
Data from the US Forest Service: Prescribed Fire Management in the South (page 26)

Using the above data, a fuel flow rate based on the basal area and the year since last burn is programmed into the model. Tests of the model show that when the basal area is held at a constant, the fuel accumulation accurately simulates the data obtained from the USFS. Also, a counter is programmed into the model that records the number of years that have passed since the most recent prescribed burn. This timer and the basal area are necessary to ensure that the fuel accumulates at the correct rate. Again, after year 20, the rate of accumulation is assumed to equilibrate with the rate of decomposition.

The amount of fuel is then used to find the fire intensity of the burn. The model uses G. M. Byram's fireline intensity equation: $I = H \cdot w \cdot r$, where:

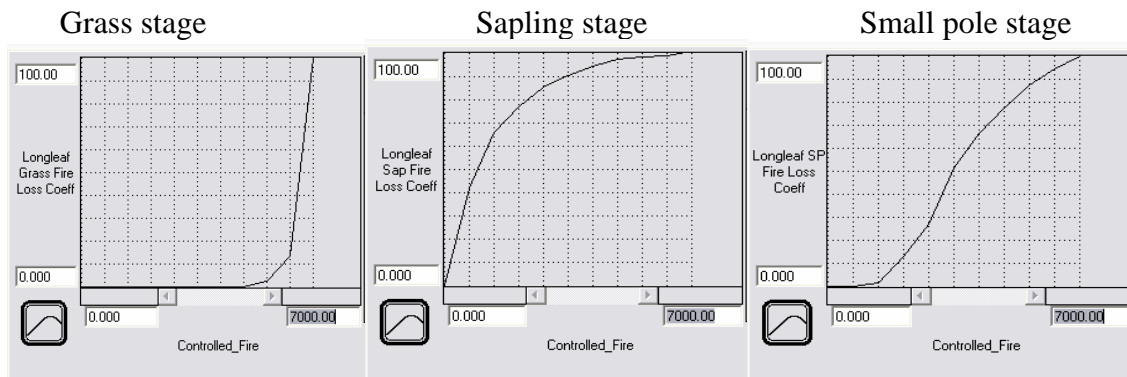
I = Byram's fireline intensity (kW/m)

H = heat of combustion (kJ/kg)

w = weight of fuel consumed per unit area (kg/m²)

r = rate of spread (m/s)

The low heat of combustion (H) varies slightly with the moisture content of the fuel. However, because low heat of combustion varies so little from fuel to fuel the value of low heat of combustion within the model is assumed to be a constant 18,000 kJ/kg. (Albini, 1976). The weight of fuel consumed per unit area (w) is calculated as previously discussed by using the USFS data. The units are converted from tons/acre to kg/m^2 . The rate of spread is equivalent to the wind speed. The wind speed is assumed to be a constant 2.5 m/s when all burns occur. The fire intensity calculated by the model using Byram's equation is directly related to longleaf mortality. As stated previously, complete annihilation of the longleaf age classes occur at a fire intensity of 7000 kW/m. Each age class responds differently to fire. For instance, longleaf saplings are somewhat fire resistant, but are more susceptible to death due to higher intensity fires. The graphical relationships between fire intensity and each age group are as follows:



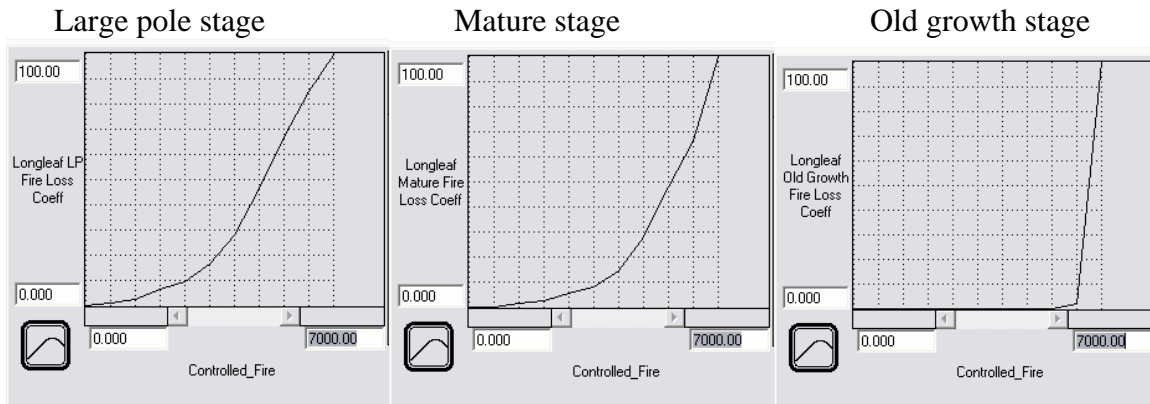


Figure 3.2 The graphical relationships between each longleaf age class fire loss coefficient and the intensity of fire. The grass stage longleaf, with no growth bud exposed, is almost as fire tolerant as the old growth age class.

Habitat Quality and RCW Fitness Modeling

The habitat quality (the physical health of the forest), coupled with the species' genetic diversity determines the fitness of the population and therefore survival. Habitat quality is the state of the physical environment. In the RCW ecosystem, habitat quality refers to the condition of a longleaf pine stand and the amount of hardwood understory within the longleaf stand. The Habitat Quality Index (HQI) is a factor of two variables within the physical environment – the number of foraging trees per bird and the hardwood understory encroachment. Both variables have an equal effect on the HQI. Habitat quality is an important aspect when managing endangered species. Not only must the habitat be healthy, but the species in question must relate to this habitat successfully. This ability of the species to relate to its habitat is referred to as the fitness of the species. Sometimes, especially when dealing with the dynamics of genetic drift, the species' fitness might change. High quality habitat might be unsuitable to the endangered species if the species' fitness decreases due to genetic drift. If the genetic diversity of the species decreases, the species might lose its ability to survive in the same

habitat in which it once thrived. This particular view of habitat quality and species' fitness helps to better explain the effects of a decrease in genetic diversity on an already suffering species.

In the model, genetic diversity is modeled using the equations from Lande, as discussed in the previous chapter. The resulting % diversity remaining is translated into a diversity factor adjustment (ranging from 0 to 1) to the HQI. This adjusted HQI represents the species' fitness. When the % diversity remaining is at high levels, the diversity factor adjustment is very close to 1, resulting in little or no negative effect on RCW fitness. When the diversity factor adjustment is low, say .3, the RCW fitness is 30% of its original value.

The understory encroachment index represents the state of the hardwood understory within the pine forest. It is a measure of the effects of mature and sapling hardwoods on the RCW foraging range. As the hardwoods increase, the hardwood understory encroachment index increases, which results in a decrease of the HQI. The foraging trees per bird is a variable that sums the old growth and mature longleaf (the trees most important to the foraging of the RCW) and divides that number by the number of adult male birds. The males are the helpers that do most of the foraging. Within the model, the females are either paired with a male for breeding purposes or they disperse. Both the understory encroachment index and the foraging trees per bird range from 0 (worst) to 0.5 (best). They are then combined to represent the HQI. Again, the HQI is then affected by the diversity factor adjustment to give the RCW fitness factor. It is this fitness factor that the model uses to affect the viability of the RCW.

Red-Cockaded Woodpecker Modeling

Perhaps the most complex section within the model is the RCW section. Since the female and male RCWs have different roles within the group, the males and females must be modeled separately. The RCW population, much like the longleaf pines, is divided into age classes. These 9 classes are the RCW fledglings and the 1 through 8 years olds, divided into 1 year classes.

Fledglings

The model assumes that 50% of the fledglings will be male; however the male to female fledgling ratio can be set by the modeler to any desired level. The first order birth rate coefficients of RCW populations usually range from 1.4 to 1.7 birds per group (per breeding pair) (USFWS, 2003). A birth rate coefficient of 1.4 fledglings per breeding pair is used in the model. This birth rate coefficient is divided between the male and female sections. Therefore, since the male to female birth ratio is 1:1 (or 50% male, 50% female), the birth rate coefficients for the both the male and female RCW sections is 0.7 (50% of 1.4). The first order death rate coefficient of fledglings is .57 for males and .68 for females (USFWS, 2003). The lower male death rate is attributed to the tendency of the male RCW to remain with the group and act as a helper. In contrast, if there are no free males to pair with, the females disperse the range before their first year in search of a new mate and new foraging areas. As most RCW populations are striving to survive on fragmented segments of longleaf stands little or no RCW pioneering is taking place, especially since it can take up to five years for a bird to excavate a new cavity. Since the model only looks at a population of RCWs in one 85 ha range, and allows no pioneering of new cavities, the dispersing females are of no concern to the model after dispersal.

The fledgling mortality is influenced by two main variables – the RCW fitness factor and what I call the “helper effect.” The RCW fitness factor affects the fledgling because of the quality of foraging range or the ability of the parent to retrieve food (modified by a decrease in genetic diversity). The helper effect relies on the number of surplus males within the population. If all the females have become breeders within the group, any excess males will become helpers. These helpers are essential in the raising of the fledglings and have even been known to assist in the incubation of eggs (USFWS, 2003). The model will allow a maximum of 3 helpers per breeding pair. Any males in excess of the result of $(3 * \text{breeding pair} + \text{breeding pair})$ will disperse and leave the model. The number of helpers divided by the number of breeding pair defines the helper effect. The helper effect then influences the fledgling survival within the model. If the fledglings survive past one year, they become adult RCW members of the 1 year old age class.

Adult RCW

Once the fledglings age up to one year old, they become adults. The adult RCW age classes consist of 1 through 8 year olds. The model assumes that when the RCW passes through the 8 year old age class, the birds die of old age. Each age class is essentially the same with slightly increased death rates in the last several years of their lifespan. Due to differences in their habits and roles within the groups, the males and females must be modeled separately. The next several paragraphs explain the male and female sections.

Female

There are two variables that influence the age classes of females – the number of males, and the RCW fitness factor. The number of males or, more specifically, the number of non breeding males present (helpers), dictates whether a female stays with the cluster or disperses out of the model. If there are helpers present and there is an empty cavity, the female and the helper will form a breeding pair. The other influence on females is the RCW fitness factor. The RCW fitness factor influences the baseline mortality coefficient of the adult female RCW in much the same manner as it influenced the fledglings' mortality. A first order baseline mortality coefficient is set at 0.21 (0.3 for the 6 and 7 year olds and 0.4 for the 8 year olds) and the RCW fitness factor, ranging from 0 to 1, directly affects the baseline mortality coefficient.

Male

There are three main variables that influence the different age classes of the male RCW – the RCW fitness factor, male RCW numbers, and the number of livable cavities. The RCW fitness factor influences the mortality coefficient of the adult male RCW in much the same manner as it influenced the fledglings. A first order baseline mortality coefficient is set at 0.2 (0.3 for the last two years) and the RCW fitness factor, ranging from 0 to 1, directly affects the baseline mortality coefficient. Also, the total number of males and breeding pairs affect the dispersal rates out of each stock. As stated, if there are already 3 males per breeding pair acting as helpers, the excess males will disperse out of the model. Another kind of dispersal is due to a constraint of cavities. If the number of males is greater than the number of cavities, the males will disperse. Since cavities take so long to excavate and the number of livable trees are few in the fragmented

populations, the birds must disperse if there are no cavities in which to live. Dispersal due to the cavity constraint only occurs when all the existing cavities are currently occupied and the number of males aging up from fledglings is greater than the male mortality rate plus the total male dispersal rate (due to male density).

The number of breeding pairs is determined by which sex of RCW has the least numbers. If the males are smaller in numbers than the females, the model will immediately disperse all the excess females. In contrast, if there are more males than females, the model will increase the number of helpers until it reaches 3 times the number of breeding pairs, then the model will disperse the remaining males. The total dispersal rate for each sex and the cavity constraint dispersal for the male are calculated across all male and female age classes and then it is weighted for each age class based on the number of birds in a particular age class. This prevents the model error of dispersing from an age class that has 0 birds.

Modeling Process

The main purpose of the model is to explore the effects of genetic drift on the health and survivability of the RCW. As stated in the previous chapters, a small population's (<500) viability is greatly affected by decreasing genetic diversity via random genetic drift. As previously discussed, a new perception of this relationship is presented in this research. Instead of assuming that genetic drift affects the RCW by simply increasing the RCW mortality, this research suggests that the decreases in genetic diversity more directly decrease fitness level of the RCW, thereby limiting their ability to survive within their habitat. Certain questions arise from this new assumption. For example, we do not know the strength of the influence that a decrease in % diversity

remaining has on the RCW fitness. This relationship is explored within the model by varying the influence of the diversity factor adjustment on the RCW fitness (model parameter). Also, it is assumed that some value of % diversity remaining will overwhelm the RCW population's ability to survive, causing extinction. The value of % diversity remaining that yields RCW extinction is not known. This value is another parameter that is explored within the model. The parameters are discussed further in the next section.

It should be noted that a reinforcing loop exists within the model which accurately represents real-world situations. This loop is as follows:

Decreasing fitness level of the species → Decreasing ability of the species to survive in its habitat (or fitness level) → Decreasing population sizes → Decreasing genetic diversity → Decreasing fitness level of the species

Parameter Relationships

The ability of the RCW to survive in its habitat is affected by many factors, including genetic diversity. It can be assumed that genetic diversity levels affect the fitness of the RCW by affecting the bird's ability to efficiently nest and forage within its habitat. A very dynamic relationship exists between RCW fitness and genetic diversity. Studies show that high genetic diversity levels have no negative effects on the viability of the population and low levels of genetic diversity result in more intense negative effects on populations. Therefore, there is an apparent direct relationship between the level of fitness and the level of genetic diversity. (This, of course, assumes that the nature of the genetic information lost is related to survivability issues; other possibilities include a direct relation to fecundity of the species which is beyond the scope of the current effort). The relationship can be graphically represented as follows:

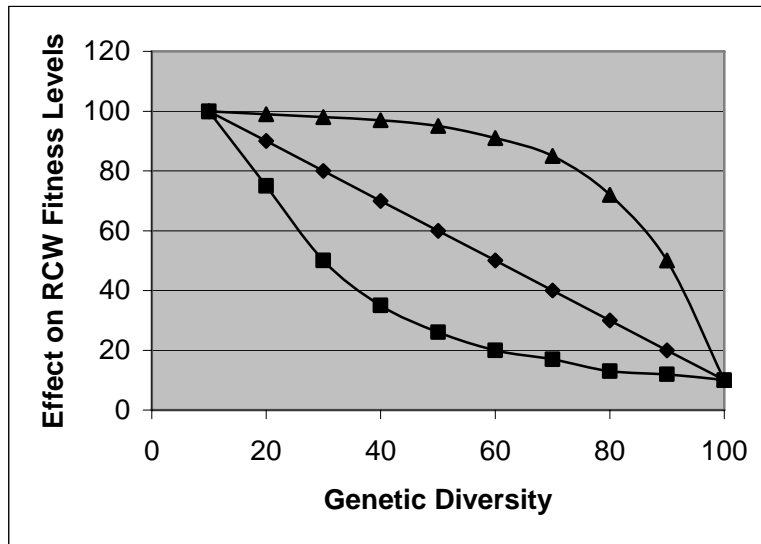


Figure 3.3 Different trend line shapes to be explored as parameter #1

The numbers on the above graph (Fig 3.3) have no purpose other than to show that a decrease in genetic diversity causes a decrease in the species' level of fitness. Although the actual lower endpoint and trend line shape of the relationship is not known, multiple functions with different slopes and shapes (as seen above) can be input into the model, enabling the modeler to assess all possible scenarios. Three trend-lines representing the intensity of the effect of genetic diversity on the level of fitness (similar to the trend lines in the figure above) are trend line possibilities within the model. Also, it can be assumed that the maximum level of % diversity remaining represents a “zero” negative effect on the RCW fitness, however, it is not known what negative effects result from lower levels of % diversity remaining. That endpoint, which represents the % diversity remaining that makes the RCW fitness decrease to an unsuitable level for the bird, is varied across a plausible intensity range during sequential simulation runs. These values are 10%, 20%, 30%, 40%, and 50% diversity remaining. With three different trend lines (the **1st parameter** within the model) and five different endpoints for each

trend line (the **2nd parameter** within the model), there are 15 possible functions representing the relationship between genetic diversity and RCW fitness.

As discussed, the population numbers affect the % diversity remaining by using the Lande equations discussed in Ch. 2. To get an accurate representation of this relationship and its effect within the model, different values of initial population number must be explored. The **3rd parameter** within the model is the initial state of the RCW population. This is a very important parameter because random genetic drift affects a small population much more than a large population. The initial RCW state is simply the initial numbers of RCWs within the population at time 0 within the model. This parameter is varied over three settings – susceptible (50 breeding pairs, 100 total members), average (200 breeding pairs, 400 total adults), and healthy (1000 breeding pairs, 2000 total adults).

Habitat quality affects the population viability. As habitat quality increases for the RCW, so does the survivability, or fitness of the RCW. To get a robust picture of all possible scenarios, four different starting values of the physical habitat quality are explored within the model. These starting values represent the initial state of the longleaf pine stand. Poor, marginal, good, and excellent are the initial values of longleaf pine. The initial longleaf state represents the **4th model parameter**. A poor initial longleaf state represents a forest where the longleaf are low in numbers. The poor setting negatively affects the RCW population by depriving them of valuable foraging range and nesting trees. The excellent setting represents a longleaf forest with abundant foraging and nesting habitat. The initial longleaf numbers usually have an affect early in the simulation time period, which is 75 years. More powerful influences, such as prescribed

burning and hardwood encroachment affects the longleaf more than the initial state of the longleaf.

Parameter Sensitivity Analysis (phase 1)

Once the model is completed, the parameters are thoroughly studied and their ranges are established (simulation phase 1). These ranges are specific to the model (each parameter being an index related to the specific model formulation) and can only be established by running the simulation and adjusting the ranges accordingly within the model. Then, parameter tests are administered and all combinations of parameter values are individually simulated and the results of each run are recorded and assessed. The initial parameter tests involve setting each variable at two extremes within their range of plausible values. With everything else held at a baseline (mid-range) value, the simulation is run and the model's sensitivity to the parameter is evaluated. This ensures proper scaling of the parameters and guarantees that the parameters are important to the model outcome. If any parameters are tested at both extremes and do not influence the outcome of the model, those parameters are examined further to ensure their validity in the model.

Full Range of Simulations (phase 2)

After running parameter extreme situations and making any necessary changes to the model, the second phase of simulations will begin. Again, the model has five varying parameters as follows:

- 1st parameter – 3 different trend lines for the “genetic diversity – intensity of effect on RCW fitness” relationship
- 2nd parameter – 5 different endpoints for the above trend-lines

3rd parameter – 3 levels of the RCW population number initial state

4th parameter – 4 levels of the longleaf pine initial state

The possible parameter combinations represent the number of simulations that will be run in phase 2. The possible parameter combinations can be found by simply multiplying the number of levels that each parameter can assume, or 3x5x3x4.

Therefore, the study demands that 180 simulations be explored within the model. Each simulation generates data on population levels, genetic diversity levels, and RCW fitness levels. Data on both end-state values and dynamic trends are structured in a manner to facilitate conclusions leading to the important scenarios to be studied during the next phase of simulations.

Ecosystem Management Practices (phase 3)

After completion of the 180 simulations across all combinations of the 4 parameters, a selected set of model scenarios are further explored by introducing prescribed burning and translocation strategies important to the RCW. The scenario selection is based on several observations. The first set of selected simulations is representative of an RCW population that is in trouble from the start. These simulations are characterized by poor initial conditions and a strong effect of genetic drift on the RCW population. The second set of simulations is chosen to represent an initially healthy RCW population that is overcome with the detrimental effects of a genetic drift. Translocation and prescribed burning are then applied to the selected scenarios. The most efficient combination of these management techniques within different scenarios give ecosystem managers valuable knowledge on proper management techniques of

RCW populations (given the existing state of the system) and how those techniques might be adjusted as time proceeds.

Also important is the full understanding of the genetic drift aspect within the RCW ecosystem. Little is known about the effects of random genetic drift on endangered populations. Hopefully, the model can give valuable insights and better understanding of the relationships between genetic drift and the viability of RCW populations. Also, the model can help researchers more accurately bound genetic drift effects by comparing the model outcome to real world situations.

Model Formulation

The model is formulated as a system of differential equations describing the dynamics of each age class of RCW and longleaf, as well as the level of fire fuel on the ground and the level of genetic diversity. Auxiliary metrics such as RCW fitness, longleaf basal area, and potential fire intensity continually change in time. The following is an example of the differential equations representing a single male RCW age class including all the factors that affect the age class:

Equation 3.1:

$$\frac{dN}{dt} = Q_{in} - (Q_{out} + Q_{dispersal} + Q_{mortality} + Q_{cavity\ overflow})$$

N is the number of individual male RCWs in a given age class. Q_{in} is the number aging up from the previous age class. The remaining components of Equation 3.1, $Q_{dispersal}$, $Q_{mortality}$, Q_{out} , $Q_{cavity\ overflow}$, and their equations, are discussed in detail in the following paragraphs.

Equation 3.2:

$$Q_{\text{total dispersal}} = \text{IF } (\text{Adult Males} - \text{Breeding Pairs}) > (3 * \text{Breeding Pair}) \\ \text{THEN } (\text{Adult Males} - \text{Breeding Pairs}) - (3 * \text{Breeding Pairs}) \text{ ELSE } (0)$$

$Q_{\text{dispersal}}$ is the number of RCW males dispersing due to lack of vacancies in the RCW social web. As previously stated, if there are 3 helper males per breeding pair within the RCW population, the males will immediately begin dispersing. Therefore, $Q_{\text{dispersal}}$ is the total male dispersal across all age classes ($Q_{\text{total dispersal}}$) weighted for each age class by the number of birds in that age class. Equation 3.2 is the Boolean statement for $Q_{\text{total dispersal}}$.

Equation 3.3: $Q_{\text{mortality}} = k_{\text{adj}} * N$

$Q_{\text{mortality}}$ in Equation 3.1 accounts for the number of birds dying due to natural causes. $Q_{\text{mortality}}$ is a first order flow defined by an adjusted mortality coefficient, k_{adj} , multiplied by the number of birds in the age class, N . The adjusted mortality coefficient is a product of the constant *baseline mortality coefficient* and the *RCW fitness effects on RCW mortality* (which has a linear relationship with the RCW fitness factor). This relationship allows the model to adjust the first order RCW mortality coefficient based on changes in the RCW fitness factor.

Equation 3.4: $Q_{\text{cavity overflow}} = \text{Logistic Term} - (Q_{\text{dispersal}} + Q_{\text{mortality}})$

Where Logistic Term = Males aging up * (total males/cavities)

$Q_{\text{cavity overflow}}$ is the dispersal of RCWs due to a lack of vacant cavities within the RCW habitat (Equation 3.4). The number of males aging up from fledglings multiplied by the total RCW males divided by the total number of natural cavities defines the

logistic trend of the dispersal due to cavity overflow. This term, minus the outflows $Q_{\text{dispersal}}$ and $Q_{\text{mortality}}$, gives the outflow due to $Q_{\text{cavity overflow}}$.

Equation 3.5:

$$Q_{\text{out}} = N - (Q_{\text{dispersal}} + Q_{\text{mortality}} + Q_{\text{cavity overflow}})$$

Q_{out} defines the number of male RCWs that age up to the next age class (Equation 3.5). Q_{out} is the number of RCWs in the age class minus the sum of $Q_{\text{dispersal}}$, $Q_{\text{mortality}}$, and $Q_{\text{cavity overflow}}$. Q_{out} is simply the number of RCWs in the age class at the end of the model derivation that have not been killed or dispersed; whatever is left simply ages up.

The model was implemented using Systems Thinking Experimental Learning Laboratory with Animation (STELLA) version 8.0 by ISEE (formerly known as High Performance Systems). The above differential equations along with equations modeling the longleaf, the hardwoods, the level of fire fuel, and the level of genetic diversity are located in Appendix A. The model flow diagrams are located in Appendix B.

IV. Data Analysis and Results

The previous chapter explains the model and the four model parameters explored within the simulated Red-cockaded Woodpecker ecosystem. All combinations of these parameters (180 simulations) were entered into the model and the outputs were recorded. Important end-state values are tabulated; these values are percent diversity remaining, total adult birds, total breeding pairs, the final RCW fitness factor, and the final number of mature and old growth longleaf pines in the bird's range.

Preliminary Sensitivity Analysis

As previously discussed, prior to running the full range of simulations, a sensitivity analysis of each parameter was performed. The sensitivity analysis ensures proper scaling of the parameters and guarantees that the parameters are important to the model outcome. The results of the sensitivity analysis are as follows:

Table 4.1 The results of the parameter sensitivity analysis

Inputs							Outputs					
Rur	Trendline Shape	Lower Value	LL Pine Initial State	RCW Initial State	Burn Cycle	# Translocated	Diversity Remaining	Breeding Pair	Total Adults	RCW Fitness Factor	Old Growth Trees	Mature Trees
1	Linear	30	Marginal	Average	6	0	69	29	66	0.55	546	662
2	Umbrella	30	Marginal	A	6	0	76	63	143	0.91	546	662
3	Bowl	30	Marginal	A	6	0	26	3	8	0	546	662
4	L	10	Marginal	A	6	0	71	36	83	0.65	546	662
5	L	20	Marginal	A	6	0	71	32	75	0.61	546	662
6	L	30	Marginal	A	6	0	69	29	66	0.55	546	662
7	L	40	Marginal	A	6	0	68	24	56	0.45	546	662
8	L	50	Marginal	A	6	0	65	18	43	0.29	546	662
9	L	30	Poor	A	6	0	64	22	50	0.47	535	673
10	L	30	Marginal	A	6	0	69	29	66	0.55	546	662
11	L	30	Good	A	6	0	73	36	83	0.6	554	651
12	L	30	Excellent	A	6	0	64	20	47	0.46	512	688
13	L	30	Marginal	Suscept	6	0	7	2	4	0	546	662
14	L	30	Marginal	Average	6	0	69	29	66	0.55	546	662
15	L	30	Marginal	Healthy	6	0	81	56	129	0.7	546	662

The results of the sensitivity analysis show that the model is very sensitive to the trend line shape of the genetic drift relationship to RCW fitness and the RCW initial state parameters. In contrast, the model is not as sensitive to the value of % diversity remaining that makes the RCW fitness decrease to an unsuitable level and the longleaf

initial state parameter. All the parameters, in some manner, affect the model in different ways, therefore, they are all deemed important inputs into the model.

The model outputs tabulated in the sensitivity analysis table show the end-state values. The initial states of the model outputs are of importance to understand the general trajectory of the output over time. The initial states are tabulated in the following table:

**Table 4.2 % diversity remaining and model parameter initial values
(prior to running the model)**

OUTPUT	INITIAL VALUE
% Diversity Remaining	100%
Breeding Pair	If S then 50 breeding pairs If A then 200 breeding pairs If H then 1000 breeding pairs
Total Adults	If S then 100 RCW adults If A then 400 RCW adults If H then 2000 RCW adults
RCW Fitness	Dependent on Diversity Adjustment Factor and Habitat Quality Index
Longleaf Old Growth Trees	If “poor” then 150 old growth trees If “marginal” then 300 old growth trees If “good” then 600 old growth trees If “excellent” then 900 old growth trees
Longleaf Mature Trees	If “poor” then 500 old growth trees If “marginal” then 1000 old growth trees If “good” then 2000 old growth trees If “excellent” then 3000 old growth trees

Demonstration of the Effectiveness of Land Management and Translocation

The full range of model outputs is tabulated in Appendix C. Prior to analysis of model outputs, the model must demonstrate the effectiveness of prescribed burning and translocation. The management techniques are applied to the simulations where the RCW numbers and the % diversity remaining are especially low. First, the simulation

results are filtered to only show those model runs with an end state % diversity remaining of less than 20% as follows:

Table 4.3 Model runs with an ending % diversity remaining value of less than 20%

Inputs							Outputs					
Run	Trendline Shape	Lower Value	LL Pine Initial State	RCW Initial State	Burn Cycle	# Translocated	Diversity Remaining	Breeding Pair	Total Adults	RCW Fitness Factor	Old Growth Trees	Mature Trees
1	L	10	Poor	S	6	0	15	3	7	0.05	535	673
4	L	10	Marginal	S	6	0	15	3	7	0.05	546	662
7	L	10	Good	S	6	0	15	3	7	0.05	554	651
10	L	10	Excellent	S	6	0	15	3	7	0.05	512	688
13	L	20	Poor	S	6	0	10	2	5	0	535	673
16	L	20	Marginal	S	6	0	11	2	5	0	546	662
19	L	20	Good	S	6	0	11	2	5	0	554	651
22	L	20	Excellent	S	6	0	11	2	5	0	512	688
25	L	30	Poor	S	6	0	7	2	4	0	535	673
28	L	30	Marginal	S	6	0	7	2	4	0	546	662
31	L	30	Good	S	6	0	7	2	4	0	554	651
34	L	30	Excellent	S	6	0	7	2	4	0	512	688
37	L	40	Poor	S	6	0	4	1	3	0	535	673
40	L	40	Marginal	S	6	0	4	1	3	0	546	662
43	L	40	Good	S	6	0	4	1	3	0	554	651
46	L	40	Excellent	S	6	0	4	1	3	0	512	688
49	L	50	Poor	S	6	0	2	1	2	0	535	673
52	L	50	Marginal	S	6	0	2	1	2	0	546	662
55	L	50	Good	S	6	0	2	1	2	0	554	651
58	L	50	Excellent	S	6	0	2	1	2	0	512	688
121	B	10	Poor	S	6	0	0	1	1	0	535	673
124	B	10	Marginal	S	6	0	0	1	1	0	546	662
127	B	10	Good	S	6	0	0	1	1	0	554	651
130	B	10	Excellent	S	6	0	0	1	1	0	512	688
133	B	20	Poor	S	6	0	0	1	1	0	535	673
136	B	20	Marginal	S	6	0	0	1	1	0	546	662
139	B	20	Good	S	6	0	0	1	1	0	554	651
142	B	20	Excellent	S	6	0	0	1	1	0	512	688
145	B	30	Poor	S	6	0	0	0	1	0	535	673
148	B	30	Marginal	S	6	0	0	0	1	0	546	662
151	B	30	Good	S	6	0	0	0	1	0	554	651
154	B	30	Excellent	S	6	0	0	0	1	0	512	673
157	B	40	Poor	S	6	0	0	0	1	0	535	673
158	B	40	Poor	A	6	0	17	2	6	0	535	673
160	B	40	Marginal	S	6	0	0	0	1	0	546	662
163	B	40	Good	S	6	0	0	0	1	0	554	651
166	B	40	Excellent	S	6	0	0	0	1	0	512	688
169	B	50	Poor	S	6	0	0	0	1	0	535	673
170	B	50	Poor	A	6	0	14	2	5	0	535	673
172	B	50	Marginal	S	6	0	0	0	1	0	546	662
175	B	50	Good	S	6	0	0	0	1	0	554	651
178	B	50	Excellent	S	6	0	0	0	1	0	512	688
179	B	50	Excellent	A	6	0	18	2	6	0	512	688

Next, with the simulations above (% diversity remaining of less than 20%) the prescribed burn frequency is increased from a 6 year cycle to a 3 year cycle. The 3 year cycle results are below:

Table 4.4 The runs from Fig 4.3 with a 3 year burn cycle instead of the baseline 6 year burn cycle

Inputs							Outputs					
Run	Trendline Shape	Lower Value	LL Pine Initial State	RCW Initial State	Burn Cycle	# Translocated	Diversity Remaining	Breeding Pair	Total Adults	RCW Fitness Factor	Old Growth Trees	Mature Trees
1	L	10	Poor	S	3	0	59	26	61	0.54	660	866
4	L	10	Marginal	S	3	0	59	27	62	0.54	690	845
7	L	10	Good	S	3	0	59	27	62	0.54	771	805
10	L	10	Excellent	S	3	0	59	27	62	0.54	829	786
13	L	20	Poor	S	3	0	56	21	49	0.45	660	866
16	L	20	Marginal	S	3	0	56	21	49	0.45	690	845
19	L	20	Good	S	3	0	56	21	49	0.45	771	805
22	L	20	Excellent	S	3	0	56	21	49	0.45	829	786
25	L	30	Poor	S	3	0	52	15	35	0.31	660	866
28	L	30	Marginal	S	3	0	52	15	35	0.31	690	845
31	L	30	Good	S	3	0	52	15	35	0.31	771	805
34	L	30	Excellent	S	3	0	52	15	35	0.31	829	786
37	L	40	Poor	S	3	0	45	9	21	0.08	660	866
40	L	40	Marginal	S	3	0	45	9	21	0.08	690	845
43	L	40	Good	S	3	0	45	9	21	0.08	771	805
46	L	40	Excellent	S	3	0	45	9	21	0.08	829	786
49	L	50	Poor	S	3	0	32	4	11	0.01	660	866
52	L	50	Marginal	S	3	0	32	4	11	0.01	690	845
55	L	50	Good	S	3	0	32	4	11	0.01	771	805
58	L	50	Excellent	S	3	0	32	4	11	0.01	829	786
121	B	10	Poor	S	3	0	1	1	2	0.01	660	866
124	B	10	Marginal	S	3	0	1	1	2	0.01	690	845
127	B	10	Good	S	3	0	1	1	2	0.01	771	805
130	B	10	Excellent	S	3	0	1	1	2	0.01	829	786
133	B	20	Poor	S	3	0	0	1	2	0.01	660	866
136	B	20	Marginal	S	3	0	0	1	2	0.01	690	845
139	B	20	Good	S	3	0	0	1	2	0.01	771	805
142	B	20	Excellent	S	3	0	0	1	2	0.01	829	786
145	B	30	Poor	S	3	0	0	1	2	0.01	660	866
148	B	30	Marginal	S	3	0	0	1	2	0.01	690	845
151	B	30	Good	S	3	0	0	1	2	0.01	771	805
154	B	30	Excellent	S	3	0	0	1	2	0.01	829	786
157	B	40	Poor	S	3	0	0	1	1	0.01	660	866
158	B	40	Poor	A	3	0	43	5	13	0.01	660	866
160	B	40	Marginal	S	3	0	0	1	1	0.01	690	845
163	B	40	Good	S	3	0	0	1	1	0.01	771	805
166	B	40	Excellent	S	3	0	0	1	1	0.01	829	786
169	B	50	Poor	S	3	0	0	1	1	0.01	660	866
170	B	50	Poor	A	3	0	36	4	10	0.01	660	866
172	B	50	Marginal	S	3	0	0	1	1	0.01	690	845
175	B	50	Good	S	3	0	0	1	1	0.01	771	805
178	B	50	Excellent	S	3	0	0	1	1	0.01	829	786
179	B	50	Excellent	A	3	0	60	9	22	0.03	829	786

Increases in RCW numbers, % diversity remaining, and mature/old growth trees can be seen in the 3 year burn cycle simulations of Table 4.4 – exactly what we would expect. The more frequent burning causes the understory encroachment to be much lower and it prepares an optimal seedbed for the regeneration of longleaf pines, both important aspects of RCW nesting and foraging.

Also, the health of the RCW population can be further increased by translocating 2 individuals per year along with the 3 year burn cycle. The results of translocating 2 individuals in conjunction with a 3 year burn can be seen below.

Table 4.5 The same runs as the previous figures using a 3 year cycle with 2 year translocation

Run	Trendline Shape	Lower Value	Inputs				Outputs					
			LL Pine Initial State	RCW Initial State	Burn Cycle	# Translocated	Diversity Remaining	Breeding Pair	Total Adults	RCW Fitness Factor	Old Growth Trees	Mature Trees
1	L	10	Poor	S	3	2	93	88	201	0.87	660	866
4	L	10	Marginal	S	3	2	93	89	203	0.87	690	845
7	L	10	Good	S	3	2	93	90	204	0.88	771	805
10	L	10	Excellent	S	3	2	93	90	205	0.89	829	786
13	L	20	Poor	S	3	2	93	86	196	0.87	660	866
16	L	20	Marginal	S	3	2	93	86	197	0.87	690	845
19	L	20	Good	S	3	2	93	87	198	0.88	771	805
22	L	20	Excellent	S	3	2	93	87	199	0.89	829	786
25	L	30	Poor	S	3	2	93	82	188	0.88	660	866
28	L	30	Marginal	S	3	2	93	83	189	0.88	690	845
31	L	30	Good	S	3	2	93	83	189	0.89	771	805
34	L	30	Excellent	S	3	2	93	83	189	0.89	829	786
37	L	40	Poor	S	3	2	93	78	177	0.88	660	866
40	L	40	Marginal	S	3	2	93	78	178	0.88	690	845
43	L	40	Good	S	3	2	93	78	178	0.88	771	805
46	L	40	Excellent	S	3	2	93	78	178	0.88	829	786
49	L	50	Poor	S	3	2	93	72	163	0.85	660	866
52	L	50	Marginal	S	3	2	93	72	164	0.85	690	845
55	L	50	Good	S	3	2	93	72	164	0.85	771	805
58	L	50	Excellent	S	3	2	93	72	164	0.85	829	786
121	B	10	Poor	S	3	2	89	15	34	0.37	660	866
124	B	10	Marginal	S	3	2	89	15	35	0.37	690	845
127	B	10	Good	S	3	2	89	15	35	0.37	771	805
130	B	10	Excellent	S	3	2	89	15	35	0.37	829	786
133	B	20	Poor	S	3	2	89	11	27	0.33	660	866
136	B	20	Marginal	S	3	2	89	11	27	0.33	690	845
139	B	20	Good	S	3	2	89	11	27	0.33	771	805
142	B	20	Excellent	S	3	2	89	11	27	0.33	829	786
145	B	30	Poor	S	3	2	88	8	20	0.27	660	866
148	B	30	Marginal	S	3	2	88	9	20	0.27	690	845
151	B	30	Good	S	3	2	88	9	20	0.27	771	805
154	B	30	Excellent	S	3	2	88	9	20	0.27	829	786
157	B	40	Poor	S	3	2	87	6	14	0.21	660	866
158	B	40	Poor	A	3	2	97	81	187	0.64	660	866
160	B	40	Marginal	S	3	2	87	6	14	0.21	690	845
163	B	40	Good	S	3	2	87	6	14	0.21	771	805
166	B	40	Excellent	S	3	2	87	6	14	0.21	829	786
169	B	50	Poor	S	3	2	85	4	10	0.16	660	866
170	B	50	Poor	A	3	2	96	71	165	0.56	660	866
172	B	50	Marginal	S	3	2	85	4	10	0.16	690	845
175	B	50	Good	S	3	2	85	4	10	0.16	771	805
178	B	50	Excellent	S	3	2	85	4	10	0.16	829	786
179	B	50	Excellent	A	3	2	98	139	323	0.63	829	786

The translocation of 2 individuals, as seen in the above simulations, shows an increase in both the % genetic diversity remaining and RCW population numbers. When

the model simulates more frequent burn cycles and RCW translocation, both the habitat quality is increased and the genetic diversity is increased.

It should be noted that the change from the *good* initial longleaf state to the *excellent* initial longleaf state causes a *decrease* in RCW numbers, % diversity remaining, and mature/old growth trees. This unexpected phenomenon is due to the heightened tree density at the excellent value for the initial longleaf parameter. The heightened level of tree density, when coupled with the prescribed burn cycle, causes very intense fires; the high intensity fires bring a higher fire mortality rate to the longleaf stand. However, when the model is run with a burn cycle of 3 years, the RCW number, % diversity remaining, and mature/old growth trees all show increases. The 3 year burn cycle is frequent enough to sustain the high density pine litter (fire fuel) without burning too hot and inhibiting growth of the pine stand.

Model Exploration for Full Set of Data and Analysis

With the model operating correctly, analysis of the model output can reveal bounds on the genetic parameters which have not been explored in previous research. The model can provide the optimal combinations of land management and translocation based on the influence of genetic drift on RCW fitness and habitat quality within the system.

Before making any observations, the genetic drift parameters (the genetic diversity relationship trend-line and value of % diversity remaining that yields unsuitable fitness levels for the RCW) were fully explored within the revised boundaries discovered in observation 1. Changing the genetic diversity parameter settings within the model changed the model outcome; however, regardless of the genetic diversity parameter

settings, the conceptual observations revealed in the model output remained the same.

Since the observations held for all genetic diversity parameter settings, the runs chosen to represent each observation were those runs that best demonstrated the observation.

Those observations are highlighted in this discussion.

Genetic Drift Observations Without Management Techniques

- *Observation 1: The most damaging “concave – up” relationship describing how genetic drift affects species survivability can be eliminated from the model due to the unrealistic model output at that trend-line setting.*

The % diversity remaining of the simulations with the trend line parameter set to represent the most damaging relationship of genetic drift on the RCW fitness (or the “concave – up”) range from 0% to 87% diversity remaining and the average is only 29% diversity remaining even at a 3 year burn cycle. These % diversity remaining numbers occur at the end of only 75 years. It has been found that most RCW populations, although small and declining, will not show this highly dramatic loss of diversity (Lennartz, 1992) over the 75 year period. This trend line magnifies the effects of genetic drift on the RCW population such that sustainable populations cannot be reached, even with a high rate of translocations. Therefore, the most damaging, or concave – up trend line shape may be dismissed from the model because that trend line shape lies outside the natural boundaries of the relationship between genetic drift and RCW fitness. The most damaging trend line relates genetic drift to the species’ survivability in a manner that is too powerful to accurately represent a real world scenario. This “low end” boundary has been established within the model. However, there is another boundary that is not well known. That boundary represents the minimal effect that genetic drift has on species fitness. There is nothing in literature or in the real world that points us toward that

minimal effect boundary except that there is no effect of genetic drift on species' survivability at all. This concept, although not probable, is not inaccurate. After all, the loss of genetic diversity due to genetic drift does not target specific alleles. The alleles that are affected by genetic drift might not be essential alleles to the species, or the affected alleles might not have anything to do with the species' survivability. For example, genetic drift might cause a species to lose some of their ability to adapt only to specific changes in their environment – say an average annual temperature change. If the species is only affected by their loss of diversity when the average annual temperature changes, and the average annual temperature never changes, the species is never affected by their loss in genetic diversity. Therefore, the minimal effect of genetic drift on species fitness is a zero effect.

- *Observation 2: When the RCW initial state is low, genetic drift dominates population dynamics regardless of ecosystem health*

When the initial RCW population parameter is set at the “susceptible” level, the initial longleaf pine state parameter has no bearing on the end-state levels of RCW genetic diversity, RCW population levels, or their trends over the 75 year period. This reveals that once the number of RCW's decline below a critical population number, the state of the foraging and cavity trees becomes irrelevant to the survival of the birds.

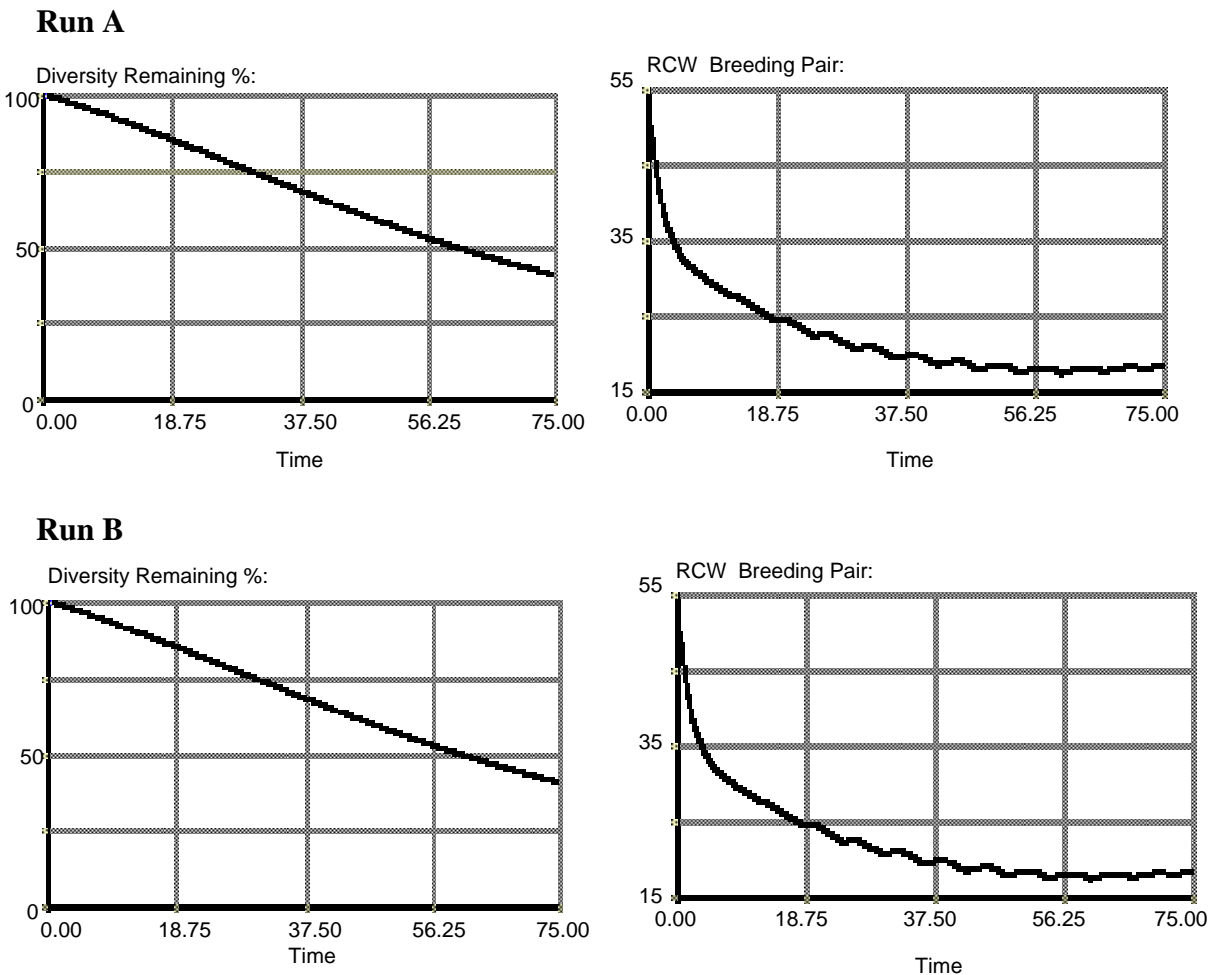


Figure 4.1 Low RCW initial state % diversity remaining and RCW breeding pair results.
Run A has an initial longleaf state of poor and Run B has an initial longleaf state of excellent

Figure 4.1 displays the results from model runs A & B. These runs, both with the initial RCW population parameter set at susceptible, have equal outputs even though their initial longleaf parameters are different. With the initial RCW set at susceptible and all else equal, Run A (Run 64) has an initial longleaf parameter setting of poor and Run B (Run 70) has an initial longleaf parameter setting of excellent. The top graphs in figure 4.1 show the % diversity remaining and the RCW breeding pair from run A. The bottom graphs show the % diversity remaining and the RCW breeding pair from run B. Despite

the differences in the initial longleaf state, both runs have equal outputs. This phenomenon is only present when the initial RCW state is low (susceptible). When the initial RCW state is low, the enhanced negative effects of genetic drift outweigh any effects that the initial longleaf state has on the health of the RCW. This demonstrates how genetic drift within small populations can potentially have a large effect on the viability of the population.

Genetic Drift Observations With the Effect of Management Techniques Under Different States of Ecosystem Health

As stated previously, burn management is a very important management tool that ecosystem managers can use to enhance the habitat, and therefore viability, of the RCW. The burning creates the park-like pine stands which are very important to RCW populations. Also important, but less frequently used, is the management technique of translocation. Again, translocation helps to offset the effects of genetic drift by bringing new, genetically diverse individuals into the breeding population.

Although both translocation and prescribed burning are effective management techniques, they are much more effective in certain situations. A comparison of these two techniques is discussed in the following observations:

- *Observation 3: Translocation is the only viable long-term strategy in recovering from a susceptible system state with low bird numbers.*

A specific group of model simulations are selected from the 180 simulations. These simulations are chosen to represent a RCW ecosystem that is in trouble from the beginning. In addition, the relationship between % diversity remaining and the RCW fitness level is a linear relationship, which is the least favorable, realistic relationship within the model (the concave - up relationship was ruled out as not well-representing a

real-world situation (see observation 1)). The value of % diversity remaining that most affects the RCW fitness level is high (set at 40%). The initial RCW state is a low value (set at susceptible). Finally, the initial longleaf state within the RCW range is at a lower value (set at poor). With the model set at the above parameters (Run #37, 0 translocated, on a 6 year burn cycle) the % diversity remaining and the number of RCW breeding pairs are as follows:

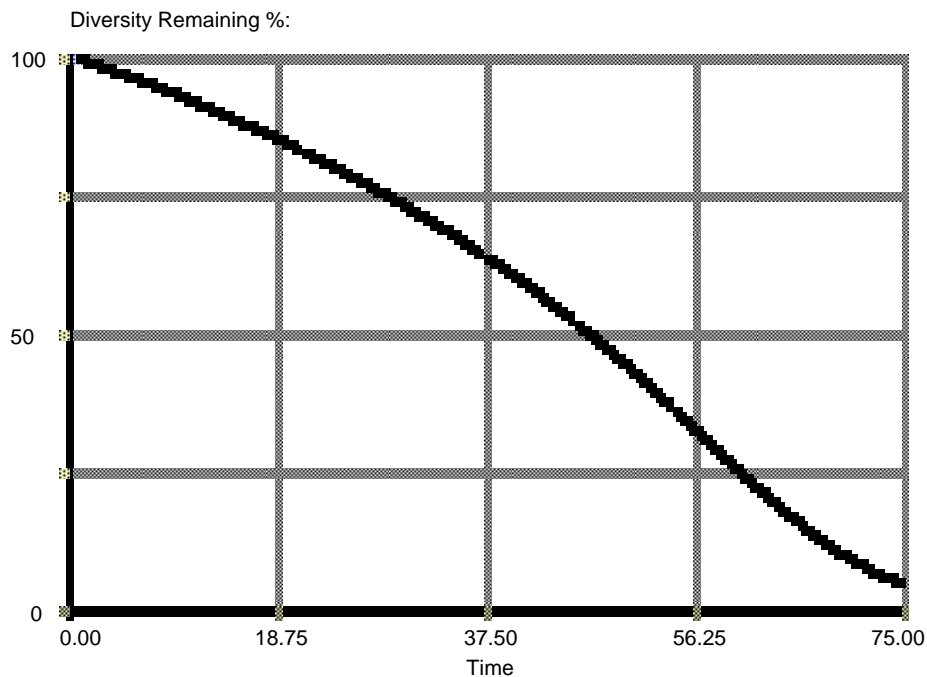


Figure 4.2 The % diversity remaining over 75 years at the initially susceptible system state with low bird numbers

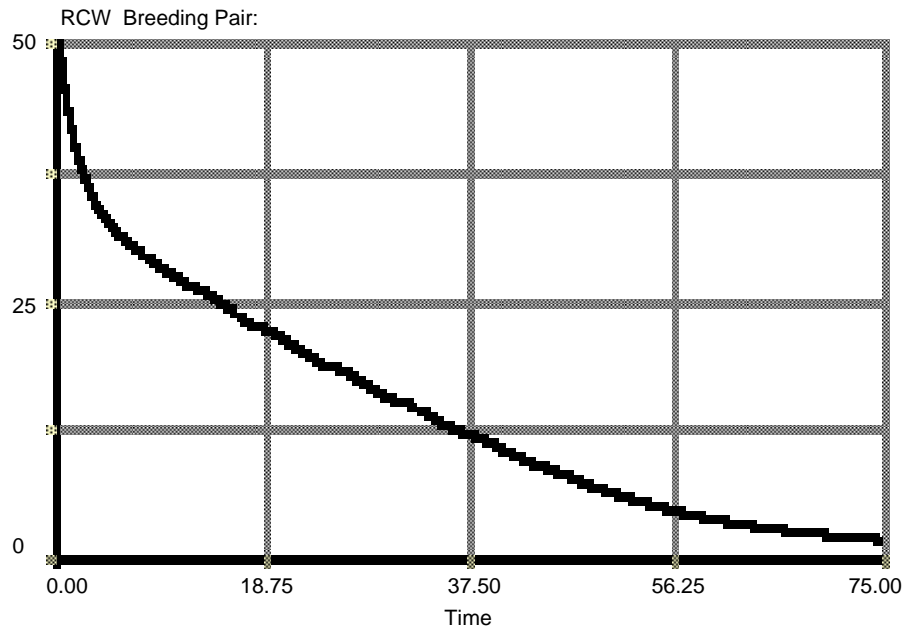


Figure 4.3 The number of RCW breeding pairs at the end of the 75 year period at the initially susceptible system state with low bird numbers.
Note the end-state value of 1 pair at the end of 75 years.

The population declines early in the model are due to fewer foraging trees per bird due to the poor longleaf initial state parameter. The susceptible initial RCW state parameter adds to the decline by increasing the negative effects of genetic drift. Also, the understory encroachment index is increased because the burn cycle is an infrequent 6 year cycle. All these factors lead to the extinction of the RCW population.

To see which method of management is more effective, the above scenario is managed using a more frequent burn cycle (line 2), and then it is managed using translocation (line 3). The 6 year burn trend line (line 1), the 3 year burn trend line (line 2), and the 2 individuals translocated trend line (line 3) are all visible on the graphs in Figure 4.4:

Scenario – sub optimal conditions

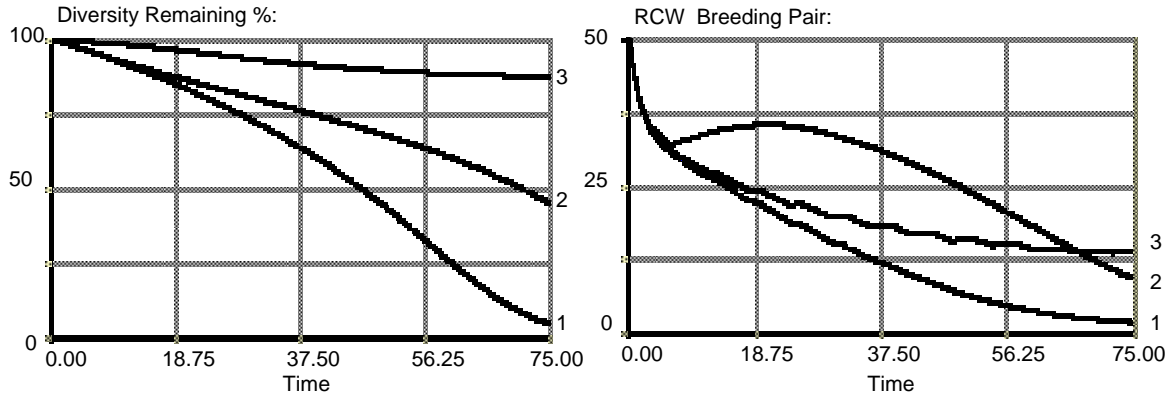


Figure 4.4 A comparison of all 3 management techniques at the initially susceptible system state with low initial bird numbers. Line 1 = no translocation at the 6 year burn. Line 2 = no translocation at the 3 year burn. Line 3 = 2 translocated at the 6 year burn

An inflection point is evident on the 3 year burn graph. While the 6 year burn line and the 2 individuals translocated line continue to decrease, the 3 year burn line increases at the 3 year point and again at the 6 year point. This phenomenon is due to prescribed burns every three years. From year 0 to year 3, the hardwoods are encroaching on the longleaf stand. The increased hardwood understory encroachment negatively affects the habitat quality index. The HQI is directly related to the mortality of RCW fledglings. By the second burn at the 6 year point, the encroaching hardwoods are eliminated. Thus, increases in the quality of the habitat and decreases in the fledgling mortality result in an increase in the number of fledglings aging to adult birds. However, by year 20, the effects of genetic drift within the small population result in population declines even with the more frequent 3 year burning cycle.

By observing the trends of the sub-optimal scenario, I conclude that the translocation of birds is the optimal solution to achieve a steady state RCW population. The 3 year burn cycle by itself is a helpful technique in the short run. However, by the

end of 75 years, the 3 year burn cycle is well on its way to extinction. Burning within this scenario seems to simply “buy time” before extinction occurs. The source of the problem in this scenario is genetic drift – a problem not solved by increasing the burn cycle. Although the boost in habitat quality due to the frequent 3 year burn cycle does help the RCW, it only helps for about 15 years. At this point the number of breeding pairs begins to decline. In contrast, translocating 2 individuals, even at the 6 year burn cycle, proves to be the only management technique that will help the birds in the long run. To support this, the model is run for a 300 year period to observe the long term trends of the scenario. Again, the baseline 6 year burn (with no translocation) is line 1, the 3 year burn (with no-translocation) is line 2, and the 6 year burn, 2 translocated is line 3:

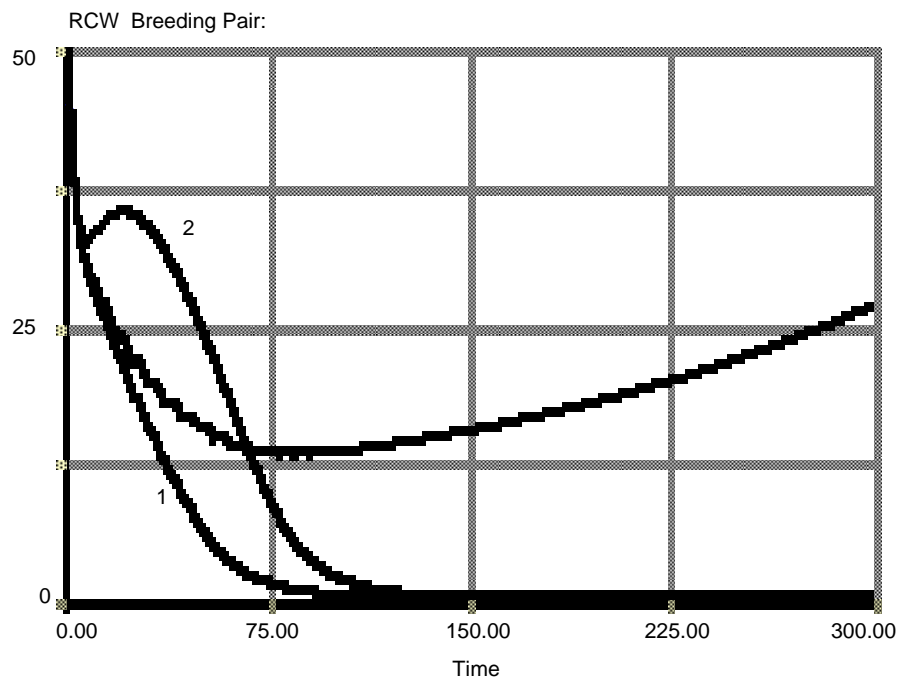


Figure 4.5 A long-term look at the effects of the management techniques

Both the 6 year burn and the 3 year burn cycle yield extinction within 150 years. However, line 2, with the 2 individuals being translocated, not only reversed the declining RCW population, but also began to increase the population by 75 years.

- *Observation 4: Proper frequency of prescribed burning is the preferred management technique when starting at a healthy system state (both short-term and long-term)*

Another group of simulations are those that begin with favorable conditions to the RCW. These simulations are characterized by a less damaging relationship between % diversity remaining and the RCW fitness level. The relationship of these situations is best represented by the concave – down shape trend line. The value of % diversity remaining that most affects the RCW fitness level is low (set at 10%). The initial RCW state is a high value (set at healthy). Finally, the initial longleaf state within the RCW range is at a high value as well (set at excellent). With the model set at the above parameters (Run #72, 0 translocation, and a 6 year burn cycle) the % diversity remaining and the number of RCW breeding pairs are as follows:

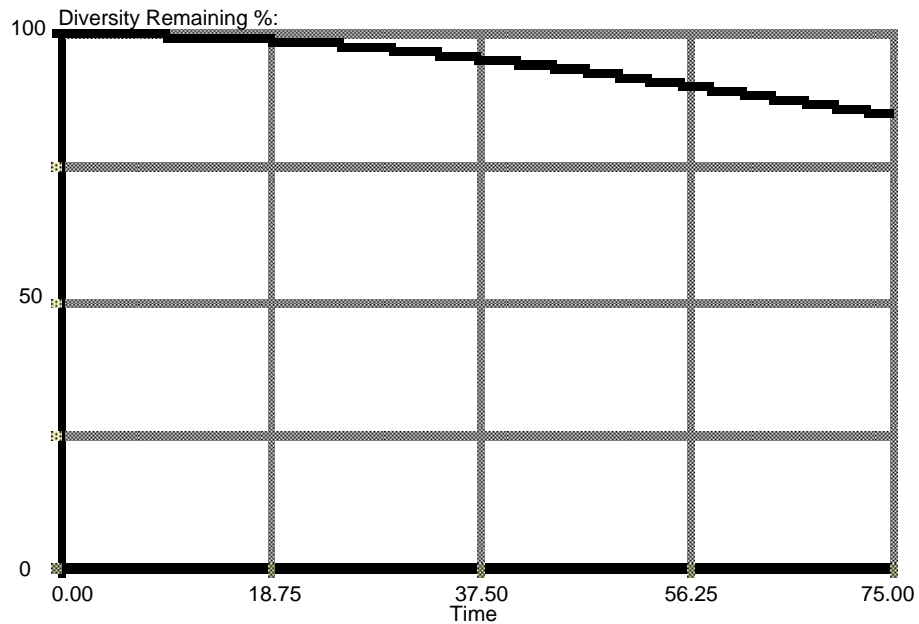


Figure 4.6 The % diversity remaining over 75 years at the initially healthy system state and healthy bird numbers

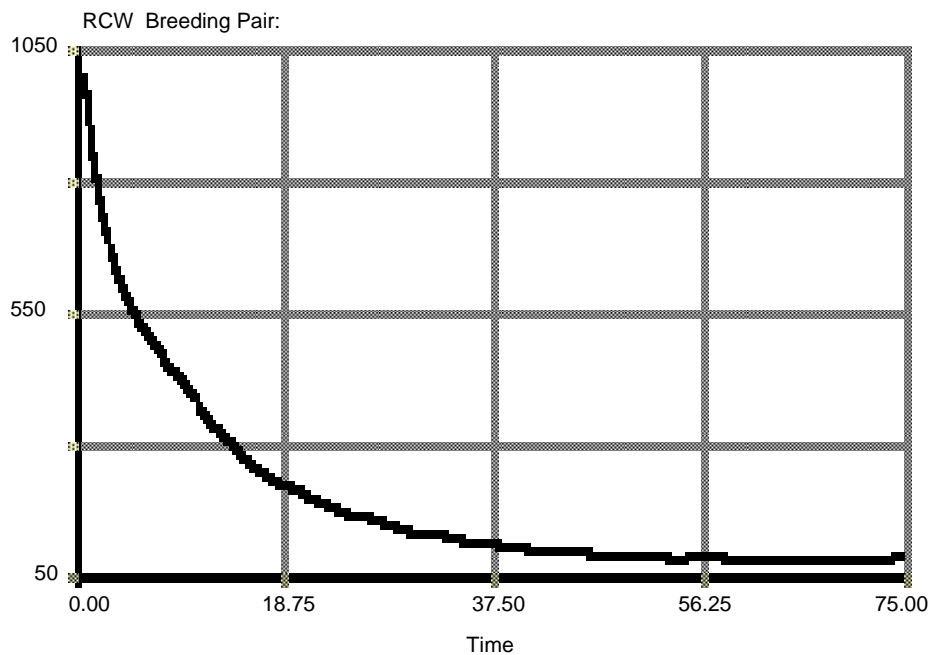


Figure 4.7 The number of RCW breeding pairs at the end of the 75 year period at the initially healthy system state and healthy RCW numbers.
Note the steady state value of 75 pairs.

The population declines early in the simulation are due to the large decline in birth rates of RCW fledglings due to the low foraging quality index. Again, during the

first six years of no burn, the hardwoods thrive and thereby lessen the quality of the foraging grounds for the RCW. Also, the foraging quality is very low because the RCW initial state is 1000 birds. This causes the foraging trees per bird (approximately 5 initially) to be well below the optimal value of 15 foraging trees per bird. The overcrowding of birds causes the foraging to be of lower quality due to competition between birds. Also, the high density of pines causes the first 6 year burn to be very intense. The intensity is enough to kill 60% of the old growth and mature longleaf, thereby causing another decrease in the number of foraging trees per bird. After a few 6 year burns, the hardwoods decline and the longleaf stand slowly begins to regenerate. The RCW numbers then reach a steady state of 170 adult birds and 75 breeding pairs.

To see which method of management is more effective, the above scenario is managed using a more frequent burn cycle, and then it is managed using translocation. The original 6 year burn trend line (line 1), the 3 year burn trend line (line 2), and the 2 individuals translocated trend line (line 3) are all visible on the graphs:

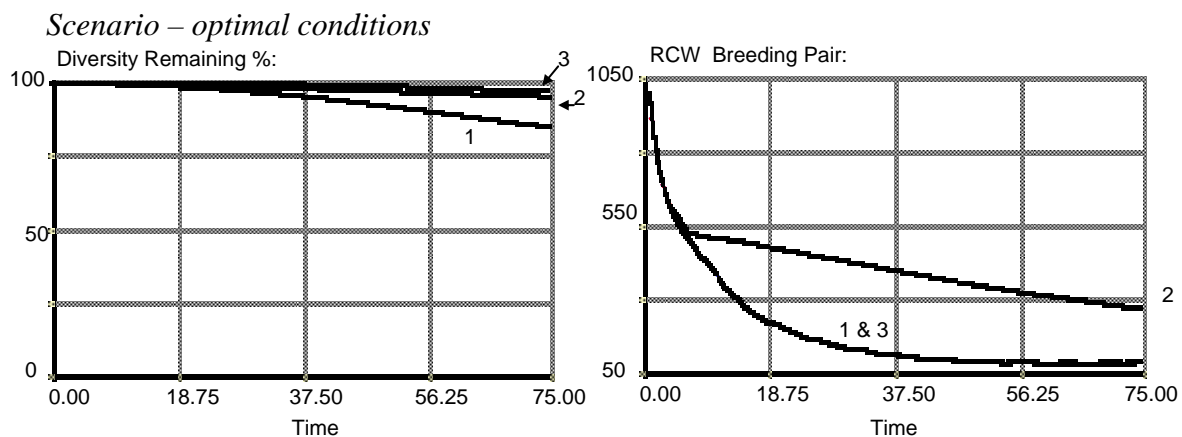


Figure 4.8 A comparison of all 3 management techniques at the initially healthy system state with healthy initial bird numbers. Line 1 = no translocation at the 6 year burn. Line 2 = no translocation at the 3 year burn. Line 3 = 2 translocated at the 6 year burn

Like observation 3, we see that there are points of inflection on the 3 year burn line at year 3 and year 6. Again, this is due to the increased quality of habitat due to the encroaching hardwoods being burned off. By the third burn at year 9, the hardwoods are eliminated and the healthier habitat positively affects the RCW fledgling survival, resulting in increases at all age classes over 75 years.

Looking at the trends of the optimal scenario, we see that there is no immediate difference between the 6 year burn cycle with no translocation and the 6 year burn cycle with 2 individuals being translocated. For the first 75 years, lines 1 and 3 follow the same path. Unlike the sub-optimal scenario, here the optimal management technique is to burn more frequently (line 2), not translocation. This is because the initial RCW population in this scenario is healthy (1000 breeding pairs initially), and therefore is not being hurt by genetic drift like the small population in the sub-optimal, so it's limiting factor is habitat quality, not genetics. If the model period is increased to 300 years, the output is as follows:

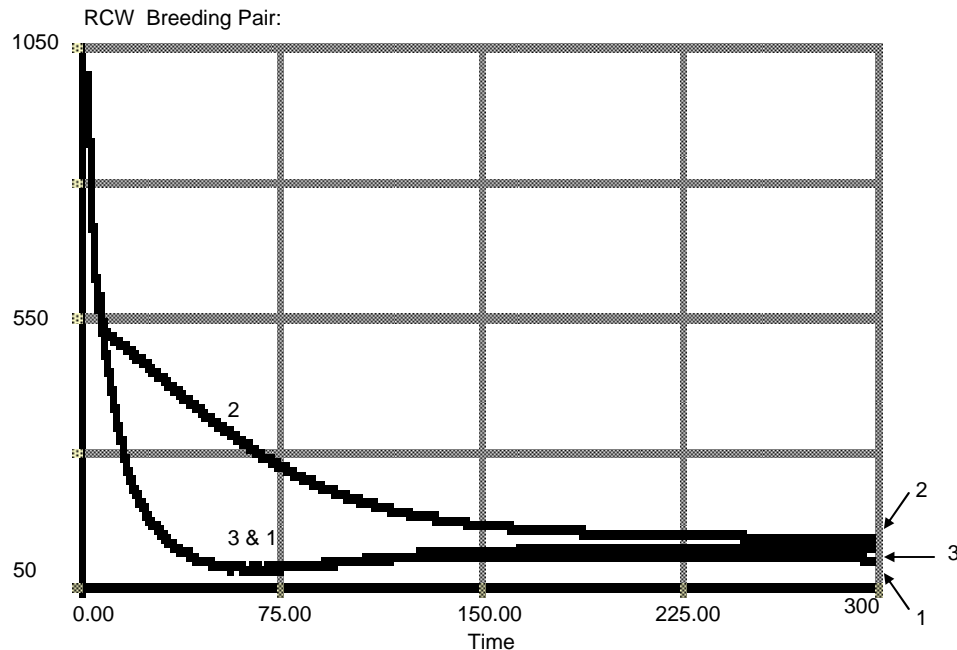


Fig 4.9 A long-term look at the effects of the management techniques

Note that the 6 year burn with 2 translocated line does separate from the 6 year burn with no translocation line in Figure 4.9. However, after 300 years, the model still produces more breeding pairs when burning is the management technique used (line 2) as opposed to translocation. Therefore, I conclude that the most effective management technique for the optimal scenario is simply to increase the frequency of prescribed burns.

- *Observation 5: A susceptible population placed in optimal habitat calls for a mixed management approach*

A third group of simulations are those that begin with a suffering RCW population (set at susceptible) living in optimal habitat conditions. This scenario could represent a situation where a small group of RCW's (100 individuals – 50 breeding pairs) are moved into a well managed habitat. These simulations are characterized by a less damaging relationship between % diversity remaining and the RCW fitness level. The

relationship of these situations is best represented by the concave – down shape trend line. Had the more damaging, linear trend line been chosen, RCW extinction would occur with the 3 year burn scenario due to the negative effects of genetic drift, as it did in observation 3. By using the less damaging, concave - down genetic drift relationship, we can allow the birds to thrive within the 3 year burn scenario. Therefore, both management techniques have the possibility of helping the RCW in the long-run.

The value of % diversity remaining that most affects the RCW fitness for the RCW is low (set at 10%). The initial RCW state is a low value (set at susceptible). Finally, the initial longleaf state within the RCW range is at a high value as well (set at excellent). With the model set at the above parameters (Run #70, 0 translocation, and a 6 year burn cycle) the % diversity remaining and the number of RCW breeding pairs are as follows:

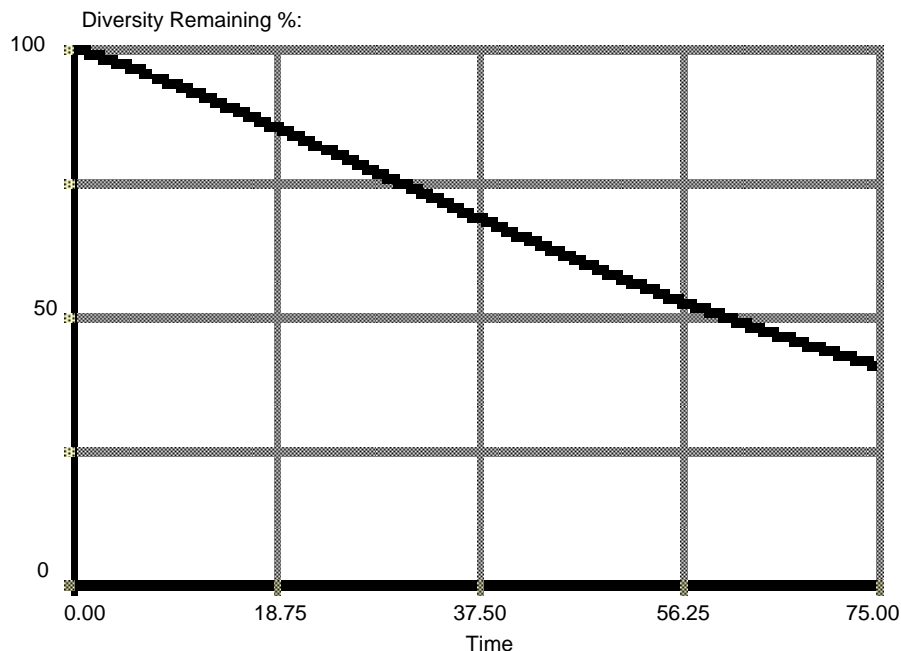


Figure 4.10 The % diversity remaining over 75 years at the healthy system and susceptible initial RCW state parameter values

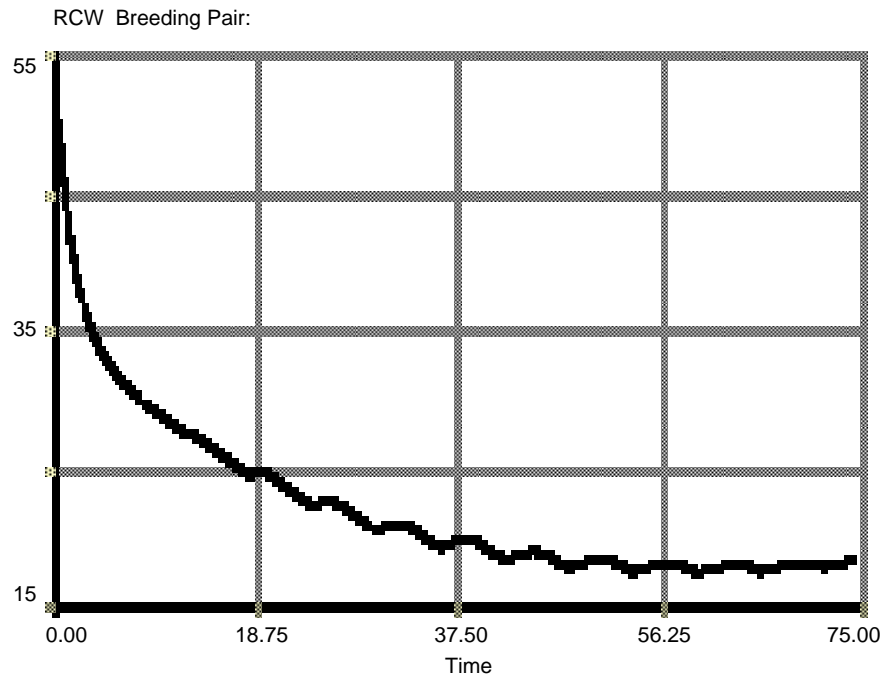


Figure 4.11 The RCW breeding pair over 75 years at the healthy system and susceptible initial RCW state parameter values

At the end of 75 years, the susceptible RCW population living in the optimal habitat seems to have become a sustaining population as seen in Figure 4.11. However, the small growth seen in the RCW population before the 75 year point is quickly reversed and total extinction occurs at the 200 year point. That extinction can be seen by simulating over a longer period of time:

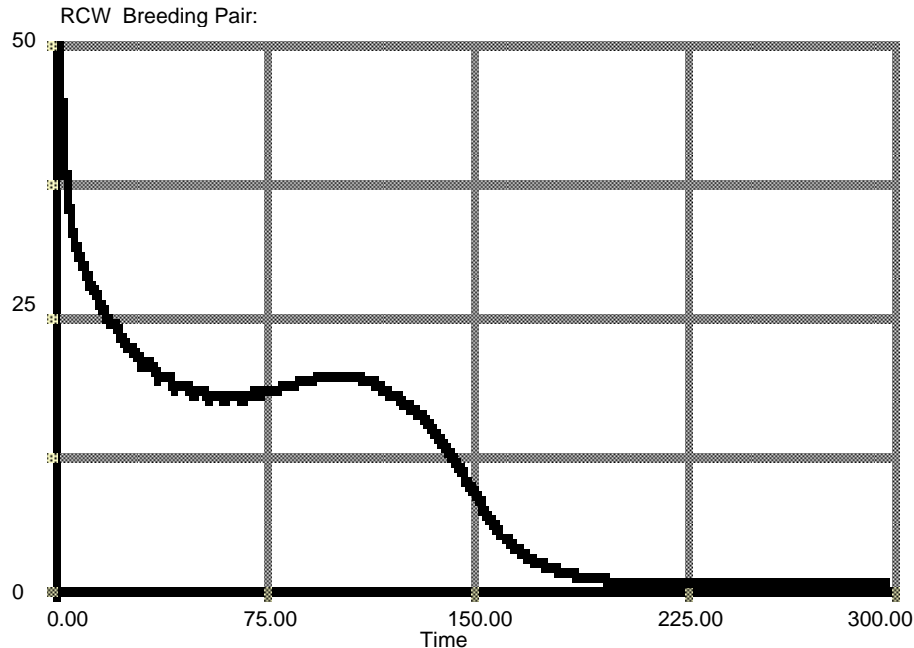


Figure 4.12 The number of RCW breeding pairs at the end of 300 years
 Note how The RCW begins to increase and then decrease
 at the 100 year point to reach total extinction by year 200.

The initial decrease in Figure 4.12 in the breeding pairs is due to the ecosystem reaching a steady state bird population. The hardwoods are burned off by the 40 year point and the breeding pairs begin to increase to reach a steady state. However, by the 100 year point, the % diversity remaining decreases enough to begin to negatively effect the survivability of the RCW, which quickly leads to extinction. This phenomenon is consistent with previous observations. Initially, the habitat is controlling the RCW numbers, much like the scenarios in observation 4. However, since the RCW population here is initially set at susceptible (unlike the scenario in observation 4, which was set at healthy), the negative effects of genetic drift soon take over and the population goes to extinction, much like the scenarios in observation 3.

Again, a management technique comparison is administered on the situation. The 6 year burn trend line (line 1), the 3 year burn trend line (line 2) and the 2 individuals translocated trend line (line 3) are all visible on the graphs:

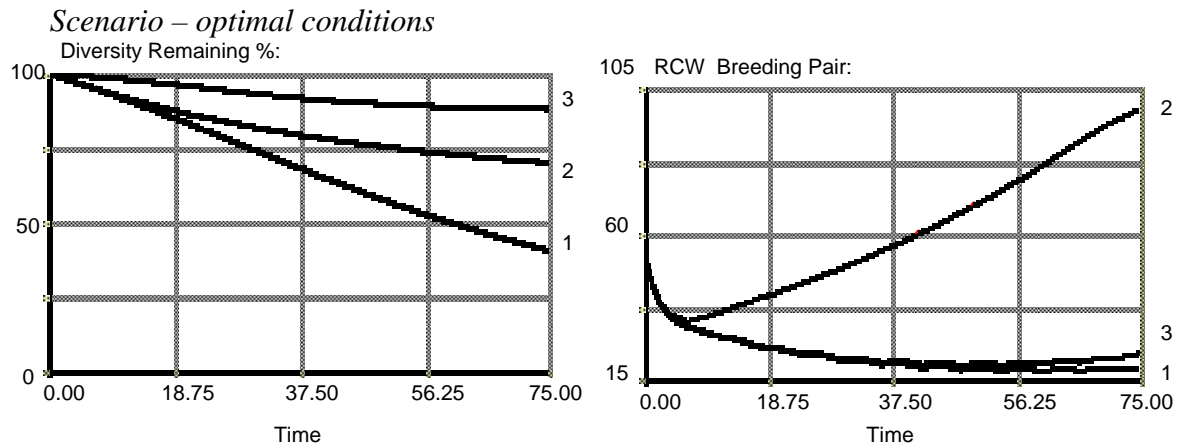


Figure 4.13 A comparison of all 3 management techniques at the initially healthy system and susceptible initial RCW state parameter values
Line 1 = no translocation at the 6 year burn. Line 2 = no translocation at the 3 year burn.
Line 3 = 2 translocated at the 6 year burn

In the short run, the increase in burn frequency from 6 years to 3 years seems to be the best management tool for the RCW population. Increases in RCW numbers are not observed when translocation is used to manage the birds. The 2-individuals translocated line produces just a few more birds (22 birds) than the no-translocation line (18 birds). However, the increase in burn frequency from 6 years to 3 years produces 99 birds. This is due to the quick decrease in hardwood understory and the healthy number of longleaf pines – which flourish under a 3 year burn cycle.

The simulation is then simulated over a 300 year duration and the results are as follows:

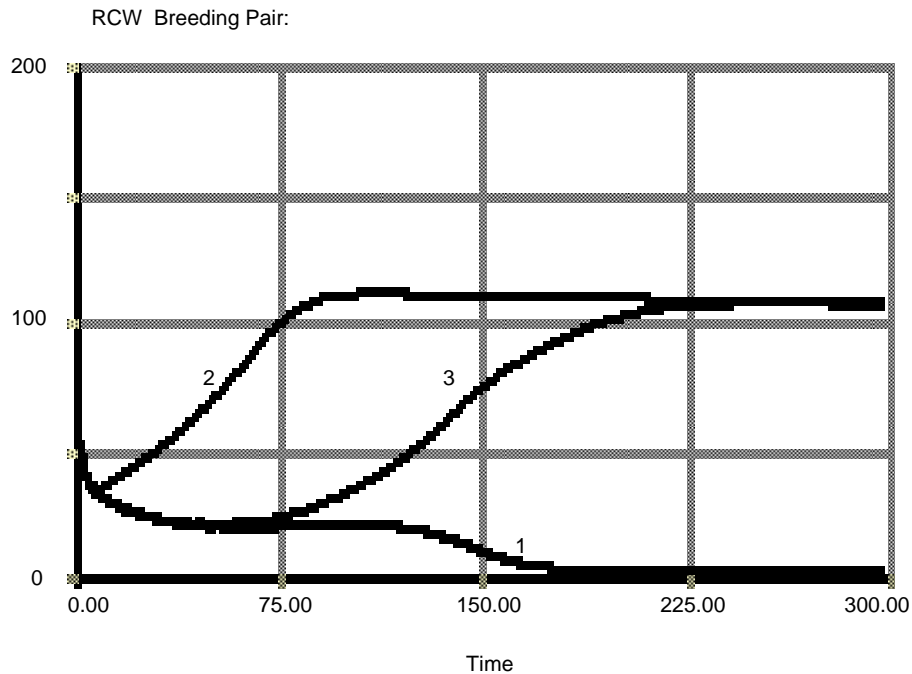


Figure 4.14 A management technique comparison over a 300 year period
 The 6 year burn, 2 individuals translocated line (line 3), with an end-state of 107 birds, finally surpasses the 3 year burn, no translocated line (line 2), which has an end state of 106 birds.

It is very interesting that, in the long run, translocating birds reaches a higher steady state than the increased burn cycles. Also, a constant decrease is observed after the 3 year burn line (line 2) reaches a maximum value in year 90. This is due to the decreasing % genetic diversity. The peak RCW population with the 3 year burn is reached because the birds have reached the carrying capacity of the habitat. However, due to the constant decreases in % diversity remaining, the fitness of the bird, is constantly decreasing – therefore the RCW population is constantly decreasing.

I conclude that since the end-state RCW population is very similar for both management techniques, a combination management technique should be used. An output graph of a combination is as follows:

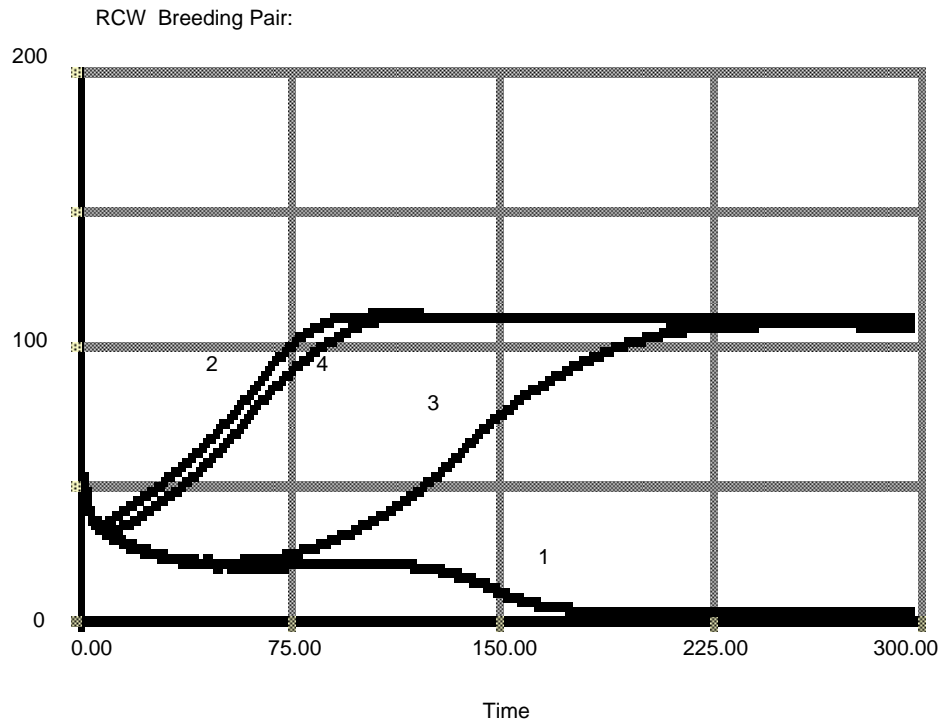


Figure 4.15 Line 4 is a combination of management techniques. It shows that a combination is the best management technique for the ecosystem.

The increase in RCW numbers due to the increased burning is very effective in the short term. However, as previously stated, after the early jumpstart in RCW numbers, the population shows a slight, but constant, decrease due to the constant loss of % diversity remaining. At this point, translocation is the key to counter act the constant decrease in genetic diversity. Line 4 in Figure 4.15 shows the trend line of a combination management technique. The burn cycle is set to 4 years and the translocation is set to only 1 individual per year. The outcome of this combination technique was a steady end-state RCW population of 110 birds – a better outcome than when the management techniques are used separately.

V. Conclusions

This work presents, for the first time, a mechanistic, dynamic model of a population within a habitat with loss of genetic diversity by genetic drift explicitly modeled and that loss feeding back to affect survivability, or fitness level, of the RCW population. This allows exploration of species viability (and recommended management strategies) under varying strengths of loss of genetic diversity effects on survivability.

Observational Conclusions

The first two model observations focus on the effects of genetic diversity on survivability and the boundaries of those effects. These observations were made prior to the introduction of any management techniques. The last 3 model observations help to guide ecosystem managers in choosing the best alternative in managing their endangered ecosystem.

The two genetic drift parameters relating diversity to RCW fitness within the model (the trend line shape and the lower value) do not have concrete literature to support them. As previously discussed, we do know that genetic drift affects the survivability of a species, but we do not know the specifics of this relationship. One method of capturing this relationship is to delve into the model outputs and decide which of those outputs do not accurately represent real-world situations. By doing this, preliminary boundaries may be placed on the genetic drift parameters. These boundaries can provide new knowledge about the relationship between genetic drift and species' survivability. Observation 1 addresses these boundaries.

Observation 1 states that the trend line representing the most damaging relationship of genetic drift on the RCW fitness level is not an accurate representation of

that relationship in any real world scenario. Even at a 3 year burn cycle, the % diversity remaining in the RCW population decreases to an average of 29% within 75 years.

Although small and declining, RCW populations will not show this enormous loss of genetic diversity (Lennartz, 1992) over a 75 year period. Even at high translocation rates, the RCW never reached a sustainable level. Therefore, the most damaging, or concave – up trend line shape may be dismissed from the model because that trend line shape lies outside the natural boundaries of the relationship between genetic drift and species' survivability. Also, the boundary that represents the minimal effect that genetic drift has on species survivability is not known. The only assumption we can make on the effect of genetic drift on species' survivability is to say that there is no effect at all. Because random genetic drift does not target specific alleles, it might not affect the species' survivability. The alleles that are deleted due to random genetic drift might be alleles that are non-essential to the survivability of the species.

Many RCW ecosystem managers believe that by manipulating the state of the physical habitat, they can reverse the declining numbers of the endangered species. RCW ecosystem management techniques are fairly constant across the southeast – prescribed burning and longleaf restoration. In many situations, longleaf restoration and a frequent burn cycle are the most efficient means to the recovery of the species. However, other situations call for management techniques that deal with the species directly, instead of dealing with the species' environment. I believe that many ecosystem managers focus their efforts on the use of land management techniques, without accounting for problems that might be directly related to the endangered species, such as

genetic diversity. The lack of genetic diversity is a problem that cannot be remedied by land management techniques.

Depending on the ecosystem state and the state of the RCW, the management techniques should vary accordingly. The model simulations of the RCW ecosystem point out that there is not one management technique that is favored over another in every situation. Ecosystem managers should assess the state of the ecosystem and choose the appropriate management technique accordingly. The following model observations provide guidance for the appropriate management techniques to be used in different ecosystem scenarios.

Observation 2 states that if the RCW population is on the brink of extinction, genetic drift will dominate regardless of the ecosystem state. This important conclusion directly applies to the RCW populations, all of which *are* very small in number. In this state, the *only* means of reviving the population is through translocation. Translocation within an endangered species might be a difficult task – there are no large populations from which managers can draw. However, by translocating birds from one small population to another, the loss of genetic diversity can be minimized by introducing a gene flow from one small population to another. By linking all small populations together via translocation, the small fragmented populations can be considered, at least on the genetic level, a large population (Stangel et al., 1992). However, until ecosystem managers understand that decreasing genetic diversity will continue to show decreases in population numbers regardless of land management, this will continue to be a problem. RCW ecosystem managers must focus on the genetic health of the bird as well as land management techniques.

Observation 3 states that when RCW numbers are susceptible, land management techniques, such as prescribed burning only provide a short-term fix to the declines in bird populations. Although land management techniques serve as methods to jump start the population in the short-term, the population will still be at the mercy of genetic drift and extinction will still occur in the long-term. Observation 2 stated that when RCW numbers are low, genetic drift dominates the system. Observation 3 states that the only fix to this domination of genetic drift is to introduce translocation and that prescribed burning will not overcome this genetic drift domination.

Observation 4 states that when the RCW and its environment are in excellent condition, the most efficient management technique is prescribed burning. At healthy numbers (1000 breeding pairs in this case) the negative effects of genetic drift are not evident; as a result the population does not suffer genetically. Therefore, if genetic drift is no longer controlling the system, the habitat becomes the most important aspect of survival. The frequent prescribed burns keep the physical habitat in good condition, causing the birds to reach a higher level of sustained population.

The scenario of a healthy population of birds living in a healthy habitat is the only scenario that requires land management techniques without translocation. This scenario is not present in the real-world. There are very few “healthy” RCW populations living in the southeastern United States. However, despite this fact, ecosystem managers continue to manage susceptible RCW ecosystems in the same manner they would manage a healthy ecosystem – using land management techniques and not regarding translocation as the most important management technique.

Observation 5 states that mixed short and long term results call for a mixed approach in managing RCW ecosystems. As stated earlier in this chapter, a frequent prescribed burn cycle can generate a quick response of growth in RCW populations. However, in the long-term, when dealing with susceptible populations, genetic drift will overtake the population and eventual extinction will occur. This is the point where translocation is important. By infusing translocation into the management plan with frequent prescribed burns, the short-term increase in population numbers caused by prescribed burning can be held at a steady state over the long-term by using translocation.

Recommendations for Future Research

Refining the model to more accurately simulate the ecosystem of the RCW is a recommendation for future researchers. Introduction of more management techniques, such as timber harvest management techniques, artificial cavity construction, and hardwood herbicide treatment in addition to prescribed burning and translocation could help ecosystem managers make better decisions about the appropriate management techniques to use in a given scenario. Since the understanding of the effects of random genetic drift is the focus of this effort, less emphasis is put on an assortment of land management tools.

Also, endangered ecosystems are similar in many aspects. Normally, the endangerment of a species is attributed to habitat quality, and in small populations, genetic diversity is an important factor. This model can be applied across a variety of endangered species and their ecosystems. Avian species, such as the recently rediscovered Ivory-Billed Woodpecker (IBW), could be inserted into this model. Slight model formulation changes would be needed to accurately represent the IBW ecosystem

and habits, but the skeletal model and the random genetic drift formulation would remain identical.

Appendix A: Model Equations

Male RCW Section

Male fledgling stock and flows:

$$d(\text{Male_RCW_Fledglings})/dt = \text{Male_Birth_Rate} - (\text{Male_Fledgling_Mortality_Rate} + \text{Males_Aging_to_1_Year_Adult})$$

$$\text{INIT Male_RCW_Fledglings} = \text{RCW_Initial_State} / 2$$

INFLOWS:

$$\text{Male_Birth_Rate} = (\text{Male_Birth_Rate_Coeff} * \text{RCW_Breeding_Pair})$$

OUTFLOWS:

$$\begin{aligned} \text{Male_Fledgling_Mortality_Rate} = & ((\text{Male_RCW_Fledglings} * \text{Adjusted_Fledg_Male_Mort_Coeff}) / \text{Helper_Effect}) \\ \text{Males_Aging_to_1_Year_Adult} = & (\text{Male_RCW_Fledglings} - \\ & \text{Male_Fledgling_Mortality_Rate}) \end{aligned}$$

Male 1 year old stock and flows:

$$d(\text{Male_1_Year_Olds})/dt = \text{Males_Aging_to_1_Year_Adult} - (\text{Male_Age_to_Year_2} + \text{Male_1_Year_Dispersal_Rate} + \text{Male_1_Year_Mortality_Rate} + \text{Cavity_OverflowM1})$$

$$\text{INIT Male_1_Year_Olds} = \text{RCW_Initial_State} / 8$$

INFLOWS:

$$\text{Males_Aging_to_1_Year_Adult} = (\text{Male_RCW_Fledglings} - \text{Male_Fledgling_Mortality_Rate})$$

OUTFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_2} = & (\text{Male_1_Year_Olds} - \\ & (\text{Male_1_Year_Mortality_Rate} + \text{Male_1_Year_Dispersal_Rate} + \\ & \text{Cavity_OverflowM1})) \\ \text{Male_1_Year_Dispersal_Rate} = & \text{Male_1_Yr_Disp} \\ \text{Male_1_Year_Mortality_Rate} = & (\text{One_Yr_Adjusted_Mort_Coeff_M} * \\ & \text{Male_1_Year_Olds}) \\ \text{Cavity_OverflowM1} = & \text{Male_Cav_Overflow_Yr_1} \end{aligned}$$

Male 2 year old stock and flows:

$$d(\text{Male_2_Year_Olds})/dt = \text{Male_Age_to_Year_2} - (\text{Male_Age_to_Year_3} +$$

$$\text{Male_2_Year_Dispersal_Rate} + \text{Male_2_Year_Mortality_Rate} + \text{Cavity_OverflowM2})$$

$$\text{INIT Male_2_Year_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_2} = & (\text{Male_1_Year_Olds} - \\ & (\text{Male_1_Year_Mortality_Rate} + \text{Male_1_Year_Dispersal_Rate} + \text{Cavity_OverflowM1})) \end{aligned}$$

OUTFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_3} = & (\text{Male_2_Year_Olds} - \\ & (\text{Male_2_Year_Dispersal_Rate} + \text{Male_2_Year_Mortality_Rate} + \text{Cavity_OverflowM2})) \end{aligned}$$

$$\text{Male_2_Year_Dispersal_Rate} = \text{Male_2_Yr_Disp}$$

$$\begin{aligned} \text{Male_2_Year_Mortality_Rate} = & \\ & (\text{Male_2_Year_Olds} * \text{Two_Yr_Adjusted_Mort_Coeff_M}) \end{aligned}$$

$$\text{Cavity_OverflowM2} = \text{Male_Cav_Overflow_Yr_2}$$

Male 3 year old stock and flows:

$$d(\text{Male_3_Year_Olds})/dt = \text{Male_Age_to_Year_3} - (\text{Male_Age_to_Year_4} +$$

$$\text{Male_3_Year_Dispersal_Rate} + \text{Male_3_Year_Mortality_Rate} + \text{Cavity_OverflowM3})$$

$$\text{INIT Male_3_Year_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_3} = & (\text{Male_2_Year_Olds} - \\ & (\text{Male_2_Year_Dispersal_Rate} + \text{Male_2_Year_Mortality_Rate} + \text{Cavity_OverflowM2})) \end{aligned}$$

OUTFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_4} = & (\text{Male_3_Year_Olds} - \\ & (\text{Male_3_Year_Dispersal_Rate} + \text{Male_3_Year_Mortality_Rate} + \text{Cavity_OverflowM3})) \end{aligned}$$

$$\text{Male_3_Year_Dispersal_Rate} = \text{Male_3_Yr_Disp}$$

$$\begin{aligned} \text{Male_3_Year_Mortality_Rate} = & \\ & (\text{Male_3_Year_Olds} * \text{Three_Yr_Adjusted_Mort_Coeff_M}) \end{aligned}$$

$$\text{Cavity_OverflowM3} = \text{Male_Cav_Overflow_Yr_3}$$

Male 4 year old stock and flows:

$$d(\text{Male_4_Year_Olds})/dt = \text{Male_Age_to_Year_4} - (\text{Male_Age_to_Year_5} +$$

$$\text{Male_4_Year_Dispersal_Rate} + \text{Male_4_Year_Mortality_Rate} + \text{Cavity_OverflowM4})$$

$$\text{INIT Male_4_Year_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_4} = & (\text{Male_3_Year_Olds} - \\ & (\text{Male_3_Year_Dispersal_Rate} + \text{Male_3_Year_Mortality_Rate} + \text{Cavity_Overflow} \\ & \text{M3})) \end{aligned}$$

OUTFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_5} = & (\text{Male_4_Year_Olds} - \\ & (\text{Male_4_Year_Dispersal_Rate} + \text{Male_4_Year_Mortality_Rate} + \text{Cavity_Overflow} \\ & \text{M4})) \end{aligned}$$

$$\text{Male_4_Year_Dispersal_Rate} = \text{Male_4_Yr_Disp}$$

$$\begin{aligned} \text{Male_4_Year_Mortality_Rate} = & \\ & (\text{Male_4_Year_Olds} * \text{Four_Yr_Adjusted_Mort_Coeff_M}) \\ \text{Cavity_OverflowM4} = & \text{Male_Cav_Overflow_Yr_4} \end{aligned}$$

Male 5 year old stock and flows:

$$\text{Male_5_Year_Olds}(t) = \text{Male_Age_to_Year_5} - (\text{Male_5_Year_Dispersal_Rate} +$$

$$\text{Male_5_Year_Mortality_Rate} + \text{Male_Age_to_Year_6} + \text{Cavity_OverflowM5})$$

$$\text{INIT Male_5_Year_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_5} = & (\text{Male_4_Year_Olds} - \\ & (\text{Male_4_Year_Dispersal_Rate} + \text{Male_4_Year_Mortality_Rate} + \text{Cavity_Overflow} \\ & \text{M4})) \end{aligned}$$

OUTFLOWS:

$$\text{Male_5_Year_Dispersal_Rate} = \text{Male_5_Yr_Disp}$$

$$\begin{aligned} \text{Male_5_Year_Mortality_Rate} = & \\ & (\text{Male_5_Year_Olds} * \text{Five_Yr_Adjusted_Mort_Coeff_M}) \end{aligned}$$

$$\begin{aligned} \text{Male_Age_to_Year_6} = & (\text{Male_5_Year_Olds} - \\ & (\text{Male_5_Year_Dispersal_Rate} + \text{Male_5_Year_Mortality_Rate} + \text{Cavity_Overflow} \\ & \text{M5})) \end{aligned}$$

$$\text{Cavity_OverflowM5} = \text{Male_Cav_Overflow_Yr_5}$$

Male 6 year old stock and flows:

$$d(\text{Male_6_Yr_Olds})/dt = \text{Male_Age_to_Year_6} - (\text{Male_6_Yr_Dispersal_Rate} +$$

$$\text{Male_6_Yr_Mortality_Rate} + \text{Male_Age_to_Year_7} + \text{Cavity_OverflowM6})$$

$$\text{INIT Male_6_Yr_Olds} = \text{RCW_Initial_State}/8$$
INFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_6} = & (\text{Male_5_Year_Olds} - \\ & (\text{Male_5_Year_Dispersal_Rate} + \text{Male_5_Year_Mortality_Rate} + \text{Cavity_Overflow} \\ & \text{M5})) \end{aligned}$$
OUTFLOWS:

$$\begin{aligned} \text{Male_6_Yr_Dispersal_Rate} &= \text{Male_6_Yr_Disp} \\ \text{Male_6_Yr_Mortality_Rate} &= \\ & (\text{Male_6_Yr_Olds} * \text{Six_Yr_Adjusted_Mort_Coeff_M}) \\ \text{Male_Age_to_Year_7} &= (\text{Male_6_Yr_Olds} - \\ & (\text{Cavity_OverflowM6} + \text{Male_6_Yr_Dispersal_Rate} + \text{Male_6_Yr_Mortality_Rate} \\ &)) \\ \text{Cavity_OverflowM6} &= \text{Male_Cav_Overflow_Yr_6} \end{aligned}$$
Male 7 year old stock and flows:

$$d(\text{Male_7_Yr_Olds})/dt = \text{Male_Age_to_Year_7} - (\text{Male_7_Yr_Mortality_Rate} +$$

$$\text{Male_7_Yr_Dispersal_Rate} + \text{Male_Age_to_Year_8} + \text{Cavity_OverflowM7})$$

$$\text{INIT Male_7_Yr_Olds} = \text{RCW_Initial_State}/8$$
INFLOWS:

$$\begin{aligned} \text{Male_Age_to_Year_7} &= (\text{Male_6_Yr_Olds} - \\ & (\text{Cavity_OverflowM6} + \text{Male_6_Yr_Dispersal_Rate} + \text{Male_6_Yr_Mortality_Rate} \\ &)) \end{aligned}$$
OUTFLOWS:

$$\begin{aligned} \text{Male_7_Yr_Mortality_Rate} &= \\ & (\text{Male_7_Yr_Olds} * \text{Seven_Yr_Adjusted_Mort_Coeff_M}) \\ \text{Male_7_Yr_Dispersal_Rate} &= \text{Male_7_Yr_Disp} \\ \text{Male_Age_to_Year_8} &= (\text{Male_7_Yr_Olds} - \\ & (\text{Cavity_OverflowM7} + \text{Male_7_Yr_Mortality_Rate} + \text{Male_7_Yr_Dispersal_Rate})) \\ \text{Cavity_OverflowM7} &= \text{Male_Cav_Overflow_Yr7} \end{aligned}$$

Male 8 year old stock and flows:

$$d(\text{Male_8_Yr_Olds})/dt = \text{Male_Age_to_Year_8} - (\text{Male_8_Yr_MortalityRate} +$$

$$\text{Male_8_Yr_Dispersal_Rate} + \text{Cavity_OverflowM8} + \text{Age_to_Life_End_M})$$

$$\text{INIT Male_8_Yr_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\text{Male_Age_to_Year_8} = (\text{Male_7_Yr_Olds} - (\text{Cavity_OverflowM7} + \text{Male_7_Yr_Mortality_Rate} + \text{Male_7_Yr_Dispersal_Rate}))$$

OUTFLOWS:

$$\text{Male_8_Yr_MortalityRate} =$$

$$(\text{Male_8_Yr_Olds} * \text{Eight_Year_Adjusted_Mort_Coeff_M})$$

$$\text{Male_8_Yr_Dispersal_Rate} = \text{Male_8_Yr_Disp}$$

$$\text{Cavity_OverflowM8} = \text{Male_Cav_Outflow_Yr_8}$$

$$\text{Age_to_Life_End_M} = (\text{Male_8_Yr_Olds} - (\text{Cavity_OverflowM8} + \text{Male_8_Yr_Dispersal_Rate} + \text{Male_8_Yr_MortalityRate}))$$

Male life end stock and flows:

$$d(\text{Male_Life_End})/dt = \text{Age_to_Life_End_M} - \text{Life_End_M}$$

$$\text{INIT Male_Life_End} = 0$$

INFLOWS:

$$\text{Age_to_Life_End_M} = (\text{Male_8_Yr_Olds} - (\text{Cavity_OverflowM8} + \text{Male_8_Yr_Dispersal_Rate} + \text{Male_8_Yr_MortalityRate}))$$

OUTFLOWS:

$$\text{Life_End_M} = \text{Male_Life_End} * \text{Male_Death_100\%}$$

Male RCW converters:

$$\text{Adjusted_Fledg_Male_Mort_Coeff} =$$

$$\text{Baseline_Male_Fledg_Mort_Rate} * \text{Fledg_Foraging_Mort_Effect}$$

$$\text{Baseline_Male_Fledg_Mort_Rate} = .57$$

$$\text{Eight_Year_Adjusted_Mort_Coeff_M} =$$

$$(\text{Eight_Yr_Baseline_Mort_Coeff_Male} * \text{Fitness_Effect_on_Mortality})$$

$$\text{Eight_Yr_Baseline_Mort_Coeff_Male} = .4$$

$$\text{Five_Yr_Adjusted_Mort_Coeff_M} = (\text{Five_Yr_Baseline_Mort_Coeff_Male} * \text{Fitness_Effect_on_Mortality})$$

$$\text{Five_Yr_Baseline_Mort_Coeff_Male} = .2$$

Four_Yr_Adjusted_Mort_Coeff_M = (Four_Yr_Baseline_Mort_Coeff_Male* Fitness_Effect_on_Mortality)
 Four_Yr_Baseline_Mort_Coeff_Male = .2
 Helpers_per_Breeding_Pair =
 IF(RCW__Breeding_Pair>0)THEN(Number__of_Helpers/RCW__Breeding_Pair)ELSE(0)
 Male_Birth_Percentage = .5
 Male_Birth_Rate_Coeff = Male_Birth_Percentage * Population_Birth_Rate_Coeff
 Male_Death_100% = 1
 Number__of_Helpers = IF((Total_Adult_Males-RCW__Breeding_Pair)>(3*RCW__Breeding_Pair))THEN(3*RCW__Breeding_Pair)ELSE(Total_Adult_Males-RCW__Breeding_Pair)
 One_Yr_Adjusted_Mort_Coeff_M = One_Yr_Baseline_Mort_Coeff_Male * Fitness_Effect_on_Mortality
 One_Yr_Baseline_Mort_Coeff_Male = .2
 Population_Birth_Rate_Coeff = 1.4
 RCW__Breeding_Pair = MIN(Total_Adult_Females,Total_Adult_Males)
 Seven_Yr_Adjusted_Mort_Coeff_M = (Seven_Yr_Baseline_Mort_Coeff_Male* Fitness_Effect_on_Mortality)
 Seven_Yr_Baseline_Mort_Coeff_Male = .3
 Six_Yr_Adjusted_Mort_Coeff_M = (Six_Yr_Baseline_Mort_Coeff_Male* Fitness_Effect_on_Mortality)
 Six_Yr_Baseline_Mort_Coeff_Male = .3
 Three_Yr_Adjusted_Mort_Coeff_M = (Three_Yr_Baseline_Mort_Coeff_Male* Fitness_Effect_on_Mortality)
 Three_Yr_Baseline_Mort_Coeff_Male = .2
 Total_Adult_Males =
 SUM(Male_1_Year_Olds,Male_2_Year_Olds,Male_3_Year_Olds,Male_4_Year_Olds,Male_5_Year_Olds,Male_6_Yr_Olds,Male_7_Yr_Olds,Male_8_Yr_Olds)
 Total_Adult_Male_Death_Rate =
 sum(Male_1_Year__Mortality_Rate,Male_2_Year_Mortality_Rate,Male_3_Year_Mortality_Rate,Male_4_Year_Mortality_Rate,Male_5_Year_Mortality_Rate,Male_6_Yr_Mortality_Rate,Male_7_Yr_Mortality_Rate,Male_8_Yr_MortalityRate)
 Two_Yr_Adjusted_Mort_Coeff_M = (Two_Yr_Baseline_Mort_Coeff_Male* Fitness_Effect_on_Mortality)
 Two_Yr_Baseline_Mort_Coeff_Male = .2

Female RCW Section

Female fledgling stock and flows:

$d(\text{Female_RCW_Fledglings})/dt = \text{Female_Birth_Rate} -$

$(\text{Female_Fledgling_Mortality_Rate} + \text{Females_Aging_to_1_Year_Adult})$

INIT Female_RCW_Fledglings = RCW_Initial_State/2

INFLOWS:

Female_Birth_Rate = (Female_Birth_Rate_Coeff * RCW__Breeding_Pair)

OUTFLOWS:

Female_Fledgling__Mortality_Rate =
((Female_RCW_Fledglings*Adjusted_Fledg_Fem_Mort_Coeff) /Helper_Effect)
Females_Aging_to_1_Year_Adult = (Female_RCW_Fledglings-
Female_Fledgling__Mortality_Rate)

Female 1 year old stock and flows:

d(Female_1_Year_Olds)/dt = Females_Aging_to_1_Year_Adult –

(Fem_Age_to__Year_2 + Female_1_Year_Dispersal_Rate +

Female_1_Year__Mortality_Rate)

INIT Female_1_Year_Olds = RCW_Initial_State/8

INFLOWS:

Females_Aging_to_1_Year_Adult = (Female_RCW_Fledglings-
Female_Fledgling__Mortality_Rate)

OUTFLOWS:

Fem_Age_to__Year_2 = (Female_1_Year_Olds-
(Female_1_Year__Mortality_Rate+Female_1_Year_Dispersal_Rate))
Female_1_Year_Dispersal_Rate = Fem_1_Yr_Wtd_Dispersal
Female_1_Year__Mortality_Rate = (One_Yr_Adjusted_Mort_Coeff_F *
Female_1_Year_Olds)

Female 2 year old stock and flows:

d(Female_2_Year_Olds)/dt = Fem_Age_to__Year_2 – (Fem_Age_to_Year_3 +

Female_2_Year_Dispersal_Rate + Female_2_Year_Mortality_Rate)

INIT Female_2_Year_Olds = RCW_Initial_State/8

INFLOWS:

Fem_Age_to__Year_2 = (Female_1_Year_Olds-
(Female_1_Year__Mortality_Rate+Female_1_Year_Dispersal_Rate))

OUTFLOWS:

Fem_Age_to_Year_3 = (Female_2_Year_Olds-
(Female_2_Year_Dispersal_Rate+Female_2_Year_Mortality_Rate))
Female_2_Year_Dispersal_Rate = Fem_2_Yr_Wtd_Dispersal
Female_2_Year_Mortality_Rate = (Female_2_Year_Olds*
Two_Yr_Adjusted_Mort_Coeff_F)

Female 3 year old stock and flows:

$d(\text{Female_3_Year_Olds})/dt = \text{Fem_Age_to_Year_3} - (\text{Fem_Age_to_Year_4} +$

$\text{Female_3_Year_Dispersal_Rate} + \text{Female_3_Year_Mortality_Rate})$

INIT Female_3_Year_Olds = RCW_Initial_State/8

INFLOWS:

Fem_Age_to_Year_3 = (Female_2_Year_Olds-
(Female_2_Year_Dispersal_Rate+Female_2_Year_Mortality_Rate))

OUTFLOWS:

Fem_Age_to_Year_4 = (Female_3_Year_Olds-
(Female_3_Year_Dispersal_Rate+Female_3_Year_Mortality_Rate))
Female_3_Year_Dispersal_Rate = Fem_3_Yr_Wtd_Dispersal
Female_3_Year_Mortality_Rate = (Female_3_Year_Olds*
Three_Yr_Adjusted_Mort_Coeff_F)

Female 4 year old stock and flows:

$d(\text{Female_4_Year_Olds})/dt = \text{Fem_Age_to_Year_4} - (\text{Fem_Age_to_Year_5} +$

$\text{Female_4_Year_Dispersal_Rate} + \text{Female_4_Year_Mortality_Rate})$

INIT Female_4_Year_Olds = RCW_Initial_State/8

INFLOWS:

Fem_Age_to_Year_4 = (Female_3_Year_Olds-
(Female_3_Year_Dispersal_Rate+Female_3_Year_Mortality_Rate))

OUTFLOWS:

Fem_Age_to_Year_5 = (Female_4_Year_Olds-
(Female_4_Year_Dispersal_Rate+Female_4_Year_Mortality_Rate))
Female_4_Year_Dispersal_Rate = Fem_4_Yr_Wtd_Dispersal
Female_4_Year_Mortality_Rate = (Female_4_Year_Olds*
Four_Yr_Adjusted_Mort_Coeff_F)

Female 5 year old stock and flows:

$$d(\text{Female_5_Year_Olds})/dt = \text{Fem_Age_to_Year_5} - (\text{Female_5_Year_Dispersal_Rate} \\ + \text{Female_5_Year_Mortality_Rate} + \text{Fem_Age_to_Year_6})$$

$$\text{INIT Female_5_Year_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\text{Fem_Age_to_Year_5} = (\text{Female_4_Year_Olds} - \\ (\text{Female_4_Year_Dispersal_Rate} + \text{Female_4_Year_Mortality_Rate}))$$

OUTFLOWS:

$$\text{Female_5_Year_Dispersal_Rate} = \text{Fem_5_Yr_Wtd_Dispersal} \\ \text{Female_5_Year_Mortality_Rate} = \\ (\text{Female_5_Year_Olds} * \text{Five_Yr_Adjusted_Mort_Coeff_F}) \\ \text{Fem_Age_to_Year_6} = (\text{Female_5_Year_Olds} - \\ (\text{Female_5_Year_Dispersal_Rate} + \text{Female_5_Year_Mortality_Rate}))$$

Female 6 year old stock and flows

$$d(\text{Female_6_Year_Olds})/dt = \text{Fem_Age_to_Year_6} - (\text{Fem_Age_to_Year_7} + \\ \text{Female_6_Year_MortalityRate} + \text{Fem_6_Yr_Dispersal_Rate})$$

$$\text{INIT Female_6_Year_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\text{Fem_Age_to_Year_6} = (\text{Female_5_Year_Olds} - \\ (\text{Female_5_Year_Dispersal_Rate} + \text{Female_5_Year_Mortality_Rate}))$$

OUTFLOWS:

$$\text{Fem_Age_to_Year_7} = (\text{Female_6_Year_Olds} - \\ (\text{Fem_6_Yr_Dispersal_Rate} + \text{Female_6_Year_MortalityRate})) \\ \text{Female_6_Year_MortalityRate} = \\ (\text{Female_6_Year_Olds} * \text{Six_Yr_Adjusted_Mort_Coeff_F}) \\ \text{Fem_6_Yr_Dispersal_Rate} = \text{Fem_6_Yr_Wtd_Dispersal}$$

Female 7 year old stock and flows:

$$d(\text{Female_7_Year_Olds})/dt = \text{Fem_Age_to_Year_7} - (\text{Fem_Age_to_Year_8} +$$

$$\text{Female_7_Year_Mortality_Rate} + \text{Fem_7_Yr_Dispersal_Rate})$$

$$\text{INIT Female_7_Year_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\text{Fem_Age_to_Year_7} = (\text{Female_6_Year_Olds} - (\text{Fem_6_Yr_Dispersal_Rate} + \text{Female_6_Year_Mortality_Rate}))$$

OUTFLOWS:

$$\text{Fem_Age_to_Year_8} = (\text{Female_7_Year_Olds} - (\text{Fem_7_Yr_Dispersal_Rate} + \text{Female_7_Year_Mortality_Rate}))$$

$$\text{Female_7_Year_Mortality_Rate} = (\text{Female_7_Year_Olds} * \text{Seven_Yr_Adjusted_Mort_Coeff_F})$$

$$\text{Fem_7_Yr_Dispersal_Rate} = \text{Fem_7_Yr_Wtd_Dispersal}$$

Female 8 year old stock and flows:

$$d(\text{Female_8_Year_Olds})/dt = \text{Fem_Age_to_Year_8} - (\text{Female_8_Year_Mortality_Rate} +$$

$$\text{Fem_8_Yr_Dispersal_Rate} + \text{Age_to_Life_End_F})$$

$$\text{INIT Female_8_Year_Olds} = \text{RCW_Initial_State}/8$$

INFLOWS:

$$\text{Fem_Age_to_Year_8} = (\text{Female_7_Year_Olds} - (\text{Fem_7_Yr_Dispersal_Rate} + \text{Female_7_Year_Mortality_Rate}))$$

OUTFLOWS:

$$\text{Female_8_Year_Mortality_Rate} = (\text{Female_8_Year_Olds} * \text{Eight_Yr_Adjusted_Mort_Coeff_F})$$

$$\text{Fem_8_Yr_Dispersal_Rate} = \text{Fem_8_Yr_Wtd_Dispersal}$$

$$\text{Age_to_Life_End_F} = (\text{Female_8_Year_Olds} - (\text{Female_8_Year_Mortality_Rate} + \text{Fem_8_Yr_Dispersal_Rate}))$$

Female Life End Stock and flows:

$$d(\text{Female_Life_End})/dt = \text{Age_to_Life_End_F} - \text{Life_End_F}$$

$$\text{INIT Female_Life_End} = 0$$

INFLOWS:

Age_to_Life_End_F = (Female_8_Year_Olds-
(Female_8_Year_Mortality_Rate+Fem_8_Yr_Dispersal_Rate))

OUTFLOWS:

Life_End_F = Female_Life_End*Female_Death_100%

Female RCW converters:

Adjusted_Fledg_Fem_Mort_Coeff = Baseline_Female_Fledg_Mort_Rate *
Fledg_Foraging_Mort_Effect
Baseline_Female_Fledg_Mort_Rate = .67
Eight_Yr_Adjusted_Mort_Coeff_F = (Eight_Yr_Baseline_Mort_Coeff_Fem* Fitness_
Effect_on_Mortality)
Eight_Yr_Baseline_Mort_Coeff_Fem = .4
Female_Birth_Percentage = 1-Male_Birth_Percentage
Female_Birth_Rate_Coeff = Female_Birth_Percentage * Population_Birth_Rate_Coeff
Female_Death_100% = 1
Five_Yr_Adjusted_Mort_Coeff_F = (Five_Yr_Baseline_Mort_Coeff_Fem* Fitness_
Effect_on_Mortality)
Five_Yr_Baseline_Mort_Coeff_Fem = .21
Four_Yr_Adjusted_Mort_Coeff_F = (Four_Yr_Baseline_Mort_Coeff_Fem* Fitness_
Effect_on_Mortality)
Four_Yr_Baseline_Mort_Coeff_Fem = .21
One_Yr_Adjusted_Mort_Coeff_F = (One_Yr_Baseline_Mort_Coeff_Fem* Fitness_
Effect_on_Mortality)
One_Yr_Baseline_Mort_Coeff_Fem = .21
Seven_Yr_Adjusted_Mort_Coeff_F = (Seven_Yr_Baseline_Mort_Coeff_Fem* Fitness_
Effect_on_Mortality)
Seven_Yr_Baseline_Mort_Coeff_Fem = .3
Six_Yr_Adjusted_Mort_Coeff_F = (Six_Yr_Baseline_Mort_Coeff_Fem* Fitness_
Effect_on_Mortality)
Six_Yr_Baseline_Mort_Coeff_Fem = .31
Three_Yr_Adjusted_Mort_Coeff_F = (Three_Yr_Baseline_Mort_Coeff_Fem* Fitness_
Effect_on_Mortality)
Three_Yr_Baseline_Mort_Coeff_Fem = .21
Total_Adult_Females =
sum(Female_1_Year_Olds,Female_2_Year_Olds,Female_3_Year_Olds,Female_4_Year_
Olds,Female_5_Year_Olds,Female_6_Year_Olds,Female_7_Year_Olds,Female_8_Year_
_Olds)
Total_Adult_Female_Death_Rate =
sum(Female_8_Year_Mortality_Rate,Female_5_Year_Mortality_Rate,Female_1_Year_
Mortality_Rate,Female_4_Year_Mortality_Rate,Female_2_Year_Mortality_Rate,Female_
_7_Year_Mortality_Rate,Female_6_Year_MortalityRate,Female_3_Year_Mortality_Rat
e)

Two_Yr_Adjusted_Mort_Coeff_F = (Two_Yr_Baseline_Mort_Coeff_Fem* Fitness_Effect_on_Mortality)
Two_Yr_Baseline_Mort_Coeff_Fem = .21

Fire Management

Fuel stock and flows:

$d(\text{Fuel})/dt = \text{Fuel_Gain} - \text{Decomposition}$

INIT Fuel = 0

INFLOWS:

Fuel_Gain = Basal_Area_Coeff

OUTFLOWS:

Decomposition = if (Controlled_Fire>0) then (10000000000) else (if
(Years_Since_Last_Burn<=20) then
((Basal_Area_Coeff*Years_Since_Last_Burn)/20) else (Basal_Area_Coeff))

Years since last burn stock and flows:

$d(\text{Years_Since_Last_Burn})/dt = \text{Time_In} - \text{Time_Out}$

INIT Years_Since_Last_Burn = 0

INFLOWS:

Time_In = 1

OUTFLOWS:

Time_Out = if (Controlled_Fire>0) then 10000000000 else 0

Fire management converters:

Amount_of_Fuel_kg_per_meter_sq = (Fuel*907)/4047

Basal_Area_Coeff = If (Longleaf_Basal_Area_sf_per_acre < 30) then (.028 *
Longleaf_Basal_Area_sf_per_acre) else (.7579 * exp(.0051 *
Longleaf_Basal_Area_sf_per_acre))

Controlled_Fire = PULSE(Fire_Potential_Intensity,First_Fire,Fire_Frequency)

Fire_Frequency = 6

Fire_Potential_Intensity = Heat_of_Combustion * Amount_of_Fuel_kg_per_meter_sq *
Wind_Speed

First_Fire = .01

Heat_of_Combustion = 18

$\text{Longleaf_Basal_Area_sf_per_acre} = \text{Longleaf_Total_Basal_Area_Sq_Feet} / \text{Range_Acreage}$
 $\text{Longleaf_Large_Pole_Average_DBH} = 12/12$
 $\text{Longleaf_Large_Pole_Ave_Basal_Area} = \pi * (\text{Longleaf_Large_Pole_Average_DBH}/2)^2$
 $\text{Longleaf_Lg_Pole_Total_Basal_Area} = \text{Longleaf_Large_Pole_31_to_60} * \text{Longleaf_Large_Pole_Ave_Basal_Area}$
 $\text{Longleaf_Mature_Average_DBH} = 18/12$
 $\text{Longleaf_Mature_Ave_Basal_Area} = \pi * (\text{Longleaf_Mature_Average_DBH}/2)^2$
 $\text{Longleaf_Mature_Total_Basal_Area} = \text{Longleaf_Mature_61_to_90} * \text{Longleaf_Mature_Ave_Basal_Area}$
 $\text{Longleaf_Old_Growth_Average_DBH} = 21/12$
 $\text{Longleaf_Old_Growth_Ave_Basal_Area} = \pi * (\text{Longleaf_Old_Growth_Average_DBH}/2)^2$
 $\text{Longleaf_Old_Growth_Total_Basal_Area} = \text{Longleaf_Old_Growth_91_to_200} * \text{Longleaf_Old_Growth_Ave_Basal_Area}$
 $\text{Longleaf_Sap_Average_Basal_Area} = \pi * (\text{Longleaf_Sap_Average_DBH}/2)^2$
 $\text{Longleaf_Sap_Average_DBH} = 2/12$
 $\text{Longleaf_Sap_Total_Basal_Area} = \text{Longleaf_Sap_Average_Basal_Area} * \text{Longleaf_Sapling_6_to_15_Yrs}$
 $\text{Longleaf_Small_Pole_Average_DBH} = 6/12$
 $\text{Longleaf_Small_Pole_Ave_Basal_Area} = \pi * (\text{Longleaf_Small_Pole_Average_DBH}/2)^2$
 $\text{Longleaf_SmPl_Total_Basal_Area_Area} = \text{Longleaf_Small_Pole_16_to_30_Yrs} * \text{Longleaf_Small_Pole_Ave_Basal_Area}$
 $\text{Longleaf_Total_Basal_Area_Sq_Feet} = \text{sum}(\text{Longleaf_Lg_Pole_Total_Basal_Area}, \text{Longleaf_Mature_Total_Basal_Area}, \text{Longleaf_Old_Growth_Total_Basal_Area}, \text{Longleaf_Sap_Total_Basal_Area}, \text{Longleaf_SmPl_Total_Basal_Area_Area})$
 $\text{Wind_Speed} = 2.5$

Genetic Drift Section

Genetic diversity stock and flows:

$d(\text{Genetic_Diversity})/dt = (\text{Diversity_from_Translocatees} +$

$\text{Diversity_from_Hybridization}) - \text{Diversity_Lost}$

$\text{INIT Genetic_Diversity} = \text{Initial_Diversity}$

INFLOWS:

$\text{Diversity_from_Translocatees} = m * (\text{Initial_Diversity} - \text{Genetic_Diversity})$

$\text{Diversity_from_Hybridization} = ((m * (1 - m)) / 2) * V_z$

OUTFLOWS:

$$\text{Diversity_Lost} = \text{Genetic_Diversity} / (2 * \text{Breeding_Individuals} + .0001)$$

Vz Term

$$d(Vz)/dt = Vz_Up - Vz_Down$$

$$\text{INIT } Vz = V_Ratio * \text{Initial_Diversity}$$

INFLOWS:

$$Vz_Up = \text{Genetic_Diversity} / (\text{Breeding_Individuals} + .0001)$$

OUTFLOWS:

$$Vz_Down = 2 * m * Vz$$

Genetic drift converters:

$$\text{Breeding_Individuals} = \text{RCW_Breeding_Pair} * 2$$

$$\text{Diversity_Remaining_}\% = (\text{Genetic_Diversity} / \text{Initial_Diversity}) * 100$$

$$\text{Initial_Diversity} = 100$$

$$m = \text{Translocatees} / (\text{Breeding_Individuals} + \text{Translocatees} + .0001)$$

$$\text{Translocatees} = 0$$

$$V_Ratio = .5$$

Longleaf Section

Longleaf grass stage stock and flows:

$$d(\text{Longleaf_Grass_Stage_0_to_5_Yrs})/dt = \text{Longleaf_Regeneration} -$$

$$(\text{Longleaf_Grass_to_Sapling} + \text{Longleaf_Grass_Mort} + \text{Longleaf_Grass_Fire_Loss})$$

INIT Longleaf_Grass_Stage_0_to_5_Yrs = IF (Longleaf_Initial_State = 1) THEN
(20000) ELSE (IF Longleaf_Initial_State = 2 THEN 40000 ELSE (IF
Longleaf_Initial_State = 3 THEN 80000 ELSE 120000))

INFLOWS:

$$\begin{aligned} \text{Longleaf_Regeneration} = & (\text{Longleaf_Offspring_per_Tree} * \\ & \text{Longleaf_Seed_Trees}) * \text{Fraction_Sunlight_Penetrated} * \\ & \text{Longleaf_Groundcover_Effects} * \text{Hardwood_Choking_Effect} \end{aligned}$$

OUTFLOWS:

$$\begin{aligned} \text{Longleaf_Grass_to_Sapling} = & \text{LL_Grass_to_Sap_Coeff} * \\ & \text{Longleaf_Grass_Stage_0_to_5_Yrs} \end{aligned}$$

$\text{Longleaf_Grass_Mort} = (\text{Bsln_Mort_Coeff_Grass} * \text{Longleaf_Grass_Stage_0_to_5_Yrs})$
 $\text{Longleaf_Grass_Fire_Loss} = \text{Longleaf_Grass_Stage_0_to_5_Yrs} * \text{Longleaf_Grass_Fire_Loss_Coeff}$

Longleaf sapling stock and flows:

$d(\text{Longleaf_Sapling_6_to_15_Yrs})/dt = \text{Longleaf_Grass_to_Sapling} -$

$(\text{Longleaf_Sap_to_Small_pole} + \text{Longleaf_Sap_Mort} + \text{Longleaf_Sap_Fire_Loss})$

INIT Longleaf_Sapling_6_to_15_Yrs = IF (Longleaf_Initial_State = 1) THEN (10000)
 ELSE (IF Longleaf_Initial_State = 2 THEN 20000 ELSE (IF Longleaf_Initial_State = 3
 THEN 40000 ELSE 60000))

INFLOWS:

$\text{Longleaf_Grass_to_Sapling} = \text{LL_Grass_to_Sap_Coeff} * \text{Longleaf_Grass_Stage_0_to_5_Yrs}$

OUTFLOWS:

$\text{Longleaf_Sap_to_Small_pole} = \text{Longleaf_Sapling_6_to_15_Yrs} * \text{LL_Sap_to_SP_Coeff}$
 $\text{Longleaf_Sap_Mort} = \text{IF} (\text{Longleaf_Grass_to_Sapling} > (\text{Bsln_Mort_Coeff_Sap} * \text{Longleaf_Sapling_6_to_15_Yrs})) \text{ THEN } ((\text{Bsln_Mort_Coeff_Sap} * \text{Longleaf_Sapling_6_to_15_Yrs}) + (\text{Longleaf_Grass_to_Sapling} - (\text{Bsln_Mort_Coeff_Sap} * \text{Longleaf_Sapling_6_to_15_Yrs}))) * \text{Longleaf_Capacity_Coeff} \text{ ELSE } (\text{Bsln_Mort_Coeff_Sap} * \text{Longleaf_Sapling_6_to_15_Yrs})$
 $\text{Longleaf_Sap_Fire_Loss} = \text{Longleaf_Sapling_6_to_15_Yrs} * \text{Longleaf_Sap_Fire_Loss_Coeff}$

$\text{Longleaf_Large_Pole_31_to_60}(t) = \text{Longleaf_Large_Pole_31_to_60}(t - dt) +$

$(\text{Longleaf_Small_to_Large_Pole} - \text{Longleaf_Large_to_Mature} -$

$\text{Longleaf_Large_Pole_Mort} - \text{Longleaf_LP_Fire_Loss}) * dt$

INIT Longleaf_Large_Pole_31_to_60 = IF (Longleaf_Initial_State = 1) THEN (2000)

ELSE (IF Longleaf_Initial_State = 2 THEN 4000 ELSE (IF Longleaf_Initial_State = 3

THEN 8000 ELSE 12000))

Longleaf small pole stock and flows:

$d(\text{Longleaf_Small_Pole_16_to_30_Yrs})/dt = \text{Longleaf_Sap_to_Small_pole} -$

$(\text{Longleaf_Small_to_Large_Pole} + \text{Longleaf_Small_Pole_Mort} +$

$\text{Longleaf_SP_Fire_Loss})$

INIT Longleaf_Small_Pole_16_to_30_Yrs = IF (Longleaf_Initial_State = 1) THEN (5000) ELSE (IF Longleaf_Initial_State = 2 THEN 10000 ELSE (IF Longleaf_Initial_State = 3 THEN 20000 ELSE 30000))

INFLOWS:

Longleaf_Sap_to_Small_pole = Longleaf_Sapling_6_to_15_Yrs *
LL_Sap_to_SP_Coeff

OUTFLOWS:

Longleaf_Small_to_Large_Pole = Longleaf_Small_Pole_16_to_30_Yrs *
LL_SP_to_LP_Coeff
Longleaf_Small_Pole_Mort = IF (Longleaf_Sap_to_Small_pole >
(Bsln_Mort_Coeff_SP * Longleaf_Small_Pole_16_to_30_Yrs)) THEN
((Bsln_Mort_Coeff_SP * Longleaf_Small_Pole_16_to_30_Yrs) +
(Longleaf_Sap_to_Small_pole - (Bsln_Mort_Coeff_SP *
Longleaf_Small_Pole_16_to_30_Yrs)) * Longleaf_Capacity_Coeff) ELSE
(Bsln_Mort_Coeff_SP * Longleaf_Small_Pole_16_to_30_Yrs)
Longleaf_SP_Fire_Loss = Longleaf_Small_Pole_16_to_30_Yrs *
Longleaf_SP_Fire_Loss_Coeff

Longleaf large pole stock and flows:

$d(\text{Longleaf_Large_Pole_31_to_60})/dt = \text{Longleaf_Small_to_Large_Pole} -$

$(\text{Longleaf_Large_to_Mature} + \text{Longleaf_Large_Pole_Mort} + \text{Longleaf_LP_Fire_Loss})$

INIT Longleaf_Large_Pole_31_to_60 = IF (Longleaf_Initial_State = 1) THEN (2000)
ELSE (IF Longleaf_Initial_State = 2 THEN 4000 ELSE (IF Longleaf_Initial_State = 3
THEN 8000 ELSE 12000))

INFLOWS:

Longleaf_Small_to_Large_Pole = Longleaf_Small_Pole_16_to_30_Yrs *
LL_SP_to_LP_Coeff

OUTFLOWS:

Longleaf_Large_to_Mature = Longleaf_Large_Pole_31_to_60 *
LL_LP_to_Mature_Coeff

Longleaf_Large_Pole_Mort = IF (Longleaf_Small_to_Large_Pole >
 (Bsln_Mort_Coeff_LP * Longleaf_Large_Pole_31_to_60)) THEN
 ((Bsln_Mort_Coeff_LP * Longleaf_Large_Pole_31_to_60) +
 (Longleaf_Small_to_Large_Pole-(Bsln_Mort_Coeff_LP *
 Longleaf_Large_Pole_31_to_60)) *Longleaf_Capacity_Coeff) ELSE
 (Bsln_Mort_Coeff_LP * Longleaf_Large_Pole_31_to_60)
 Longleaf_LP_Fire_Loss = Longleaf_Large_Pole_31_to_60 *
 Longleaf_LP_Fire_Loss_Coeff

Longleaf mature stock and flows:

$d(\text{Longleaf_Mature}_{61_to_90})/dt = \text{Longleaf_Large_to_Mature} -$

$(\text{Longleaf_Mature_Mort} + \text{Longleaf_Mature_to_Old_Growth} +$

$\text{Longleaf_Mature_Fire_Loss})$

INIT Longleaf__Mature_61_to_90 = IF (Longleaf_Initial_State = 1) THEN (500) ELSE
 (IF Longleaf_Initial_State = 2 THEN 1000 ELSE (IF Longleaf_Initial_State = 3 THEN
 2000 ELSE 3000))

INFLOWS:

Longleaf_Large_to_Mature = Longleaf_Large_Pole_31_to_60 *
 LL_LP_to_Mature_Coeff

OUTFLOWS:

Longleaf_Mature_Mort = IF (Longleaf_Large_to_Mature >
 (Bsln_Mort_Coeff_Mat * Longleaf__Mature_61_to_90)) THEN
 ((Bsln_Mort_Coeff_Mat * Longleaf__Mature_61_to_90) +
 (Longleaf_Large_to_Mature-(Bsln_Mort_Coeff_Mat *
 Longleaf__Mature_61_to_90)) *Longleaf_Capacity_Coeff) ELSE
 (Bsln_Mort_Coeff_Mat * Longleaf__Mature_61_to_90)
 Longleaf_Mature_to_Old_Growth = Longleaf__Mature_61_to_90 *
 LL_Mature_to_OG_Coeff
 Longleaf_Mature_Fire_Loss = Longleaf_Mature_Fire_Loss_Coeff *
 Longleaf__Mature_61_to_90

Longleaf old growth stock and flows:

$d(\text{Longleaf_Old_Growth}_{91_to_200})/dt = \text{Longleaf_Mature_to_Old_Growth} -$

$(\text{Longleaf_Life_Cycle_End} + \text{Longleaf_Old_Growth_Mort} +$

$\text{Longleaf_Old_Growth_Fire_Loss})$

INIT Longleaf_Old_Growth_91_to_200 = IF (Longleaf_Initial_State = 1) THEN (150)
 ELSE (IF Longleaf_Initial_State = 2 THEN 300 ELSE (IF Longleaf_Initial_State = 3
 THEN 600 ELSE 900))

INFLOWS:

Longleaf_Mature_to_Old_Growth = Longleaf__Mature_61_to_90 *
 LL_Mature_to_OG_Coeff

OUTFLOWS:

Longleaf_Life_Cycle_End = Longleaf_Old_Growth_91_to_200 *
 LL_OG_Life__End_Coeff
 Longleaf_Old_Growth_Mort = IF (Longleaf_Mature_to_Old_Growth >
 (Bsln_Mort_Coeff_OG * Longleaf_Old_Growth_91_to_200)) THEN
 ((Bsln_Mort_Coeff_OG * Longleaf_Old_Growth_91_to_200) +
 (Longleaf_Mature_to_Old_Growth-(Bsln_Mort_Coeff_OG *
 Longleaf_Old_Growth_91_to_200)) *Longleaf_Capacity_Coeff) ELSE
 (Bsln_Mort_Coeff_OG * Longleaf_Old_Growth_91_to_200)
 Longleaf_Old_Growth_Fire_Loss = Longleaf_Old_Growth_91_to_200 *
 Longleaf_Old_Growth_Fire_Loss_Coeff

Longleaf converters:

Bsln_Mort_Coeff_Grass = .2
 Bsln_Mort_Coeff_LP = .08
 Bsln_Mort_Coeff_Mat = .03
 Bsln_Mort_Coeff_OG = .03
 Bsln_Mort_Coeff_Sap = .15
 Bsln_Mort_Coeff_SP = .11
 LL_Grass_to_Sap_Coeff = .2
 LL_LP_to_Mature_Coeff = 1/30
 LL_Mature_to_OG_Coeff = 1/30
 LL_OG_Life__End_Coeff = 1/110
 LL_Sap_to_SP_Coeff = .1
 LL_SP_to_LP_Coeff = 1/15
 Longleaf_Adult_Trees = .75* Longleaf_Small_Pole_16_to_30_Yrs +
 Longleaf_Large_Pole_31_to_60 + Longleaf__Mature_61_to_90 +
 Longleaf_Old_Growth_91_to_200
 Longleaf_Capacity = 22920
 Longleaf_Capacity_Coeff = (Longleaf_Trees / Longleaf_Capacity) / 5
 Longleaf_Offspring_per_Tree = 15
 Longleaf_Seed_Trees = .25 * Longleaf_Large_Pole_31_to_60 +
 Longleaf__Mature_61_to_90 + .5 * Longleaf_Old_Growth_91_to_200
 Longleaf_Trees = Longleaf_Sapling_6_to_15_Yrs + Longleaf_Adult_Trees
 Longleaf_Tree_Density = Longleaf_Adult_Trees / Range_Acreage

Range_Acreage = 210

Hardwood Section

Hardwood mature stock and flows:

$$d(\text{Hardwood_Mature})/dt = \text{Hardwood_Sap_to_Mature} - (\text{Hardwood_Life_End} + \text{Hardwood_Mature_Mort} + \text{HW_Mat_Fire_Loss})$$

INIT Hardwood_Mature = 100

INFLOWS:

$$\text{Hardwood_Sap_to_Mature} = \text{Hardwood_Sapling} * \text{HW_Sap_to_Mature_Coeff}$$

OUTFLOWS:

$$\text{Hardwood_Life_End} = \text{Hardwood_Mature} * \text{HW_Mature_Death_Coeff}$$
$$\text{Hardwood_Mature_Mort} = \text{Hardwood_Mature_Mort_Coeff} * \text{Hardwood_Mature}$$
$$\text{HW_Mat_Fire_Loss} = \text{Hardwood_Mature} * \text{Hardwood_Fire_Loss_Coeff}$$

Hardwood sapling stock and flows:

$$d(\text{Hardwood_Sapling})/dt = \text{Hardwood_Regeneration} - (\text{Hardwood_Sapling_Mort} + \text{Hardwood_Sap_to_Mature} + \text{HW_Sap_Fire_Loss})$$

INIT Hardwood_Sapling = 600

INFLOWS:

$$\text{Hardwood_Regeneration} =$$
$$\text{Hardwood_Mature} * \text{Hardwood_Seed_Survival_Per_Mature_Tree}$$

OUTFLOWS:

$$\text{Hardwood_Sapling_Mort} = \text{Hardwood_Sap_Mort_Coeff} * \text{Hardwood_Sapling}$$
$$\text{Hardwood_Sap_to_Mature} = \text{Hardwood_Sapling} * \text{HW_Sap_to_Mature_Coeff}$$
$$\text{HW_Sap_Fire_Loss} = \text{Hardwood_Sapling} * \text{Hardwood_Fire_Loss_Coeff}$$

Hardwood Converters:

$$\text{Hardwood_Density} = \text{Hardwood_Mature_Den} + \text{Hardwood_Sapling_Den}$$
$$\text{Hardwood_Mature_Den} = \text{Hardwood_Mature} / \text{Range_Acreage}$$
$$\text{Hardwood_Sapling_Den} = \text{Hardwood_Sapling} / \text{Range_Acreage}$$
$$\text{HW_Mature_Death_Coeff} = 1/7$$
$$\text{HW_Sap_to_Mature_Coeff} = 1/6$$

Habitat Quality and RCW Fitness Formulation Section

HQI & RCW Fitness converters:

ForageTrees_per_Bird = (Longleaf_Old_Growth_91_to_200 +
Longleaf__Mature_61_to_90) / Total_Adult_Males
RCW_Fitness = Habitat_Quality_Index * Diversity_Factor_Adjustment
Habitat_Quality_Index = Foraging_Quality_Index + Understory_Encroachment_Index
Hardwood_Understory_Encroachment = (.75 * Hardwood_Mature) + Hardwood_Sapling

RCW Cavity Section

Natural cavity stock and converters:

$D(\text{Natural_Cavities})/dt = \text{Artificial_Cavities_Constructed} - \text{Cavity_Loss}$

INIT Natural_Cavities = IF Preset_Natural_Cavities > Longleaf_Old_Growth_91_to_200
THEN Longleaf_Old_Growth_91_to_200 ELSE Preset_Natural_Cavities

INFLOWS:

Artificial_Cavities_Constructed = Art_Cavities_Number

OUTFLOWS:

Cavity_Loss = IF (Longleaf_Old_Growth_91_to_200 < Natural_Cavities) THEN
(Net_OG/DT) ELSE (0)

Weighted cavity overflow, RCW dispersal, and logistic term converters:

Art_Cavities_Number = 0
Fem_1_Yr_Wtd_Dispersal =
Total_Female_Dispersal*(Female_1_Year_Olds/(Total_Adult_Females+.0001))
Fem_2_Yr_Wtd_Dispersal =
Total_Female_Dispersal*(Female_2_Year_Olds/(Total_Adult_Females+.0001))
Fem_3_Yr_Wtd_Dispersal =
Total_Female_Dispersal*(Female_3_Year_Olds/(Total_Adult_Females+.0001))
Fem_4_Yr_Wtd_Dispersal =
Total_Female_Dispersal*(Female_4_Year_Olds/(Total_Adult_Females+.0001))
Fem_5_Yr_Wtd_Dispersal =
Total_Female_Dispersal*(Female_5_Year_Olds/(Total_Adult_Females+.0001))
Fem_6_Yr_Wtd_Dispersal =
Total_Female_Dispersal*(Female_6_Year_Olds/(Total_Adult_Females+.0001))
Fem_7_Yr_Wtd_Dispersal =
Total_Female_Dispersal*(Female_7_Year_Olds/(Total_Adult_Females+.0001))
Fem_8_Yr_Wtd_Dispersal =
Total_Female_Dispersal*(Female_8_Year_Olds/(Total_Adult_Females+.0001))

```

Logistic_Term =
(Males_Aging_to_1_Year_Adult)*(Total_Adult_Males/Natural_Cavities)
Male_1_Yr_Disp = (Male_1_Yr_Wtd_Conversion*Total_Male_Dispersal)
Male_1_Yr_Wtd_Conversion = Male_1_Year_Olds/(Total_Adult_Males + .001)
Male_2_Yr_Disp = (Male_2_Yr_Wtd_Conversion*Total_Male_Dispersal)
Male_2_Yr_Wtd_Conversion = Male_2_Year_Olds/(Total_Adult_Males+.001)
Male_3_Yr_Disp = (Male_3_Yr_Wtd_Conversion*Total_Male_Dispersal)
Male_3_Yr_Wtd_Conversion = Male_3_Year_Olds/(Total_Adult_Males+.001)
Male_4_Yr_Disp = (Male_4_Yr_Wtd_Conversion*Total_Male_Dispersal)
Male_4_Yr_Wtd_Conversion = Male_4_Year_Olds/(Total_Adult_Males+.001)
Male_5_Yr_Disp = (Male_5_Yr_Wtd_Conversion*Total_Male_Dispersal)
Male_5_Yr_Wtd_Conversion = Male_5_Year_Olds/(Total_Adult_Males+.001)
Male_6Yr_Wtd_Conversion = Male_6_Yr_Olds/(Total_Adult_Males+.001)
Male_6_Yr_Disp = (Male_6Yr_Wtd_Conversion*Total_Male_Dispersal)
Male_7_Yr_Disp = (Male_7_Yr_Wtd_Conversion*Total_Male_Dispersal)
Male_7_Yr_Wtd_Conversion = Male_7_Yr_Olds/(Total_Adult_Males+.001)
Male_8_Yr_Disp = (Male_8_Yr_Wtd_Conversion*Total_Male_Dispersal)
Male_8_Yr_Wtd_Conversion = Male_8_Yr_Olds/(Total_Adult_Males+.001)
Male_Cav_Outflow_Yr_8 = (Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal)*Male_8_Yr_Wtd_Conversion
Male_Cav_Overflow_Yr7 = (Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal)*Male_7_Yr_Wtd_Conversion
Male_Cav_Overflow_Yr_1 = (Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal)*Male_1_Yr_Wtd_Conversion
Male_Cav_Overflow_Yr_3 = (Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal)*Male_3_Yr_Wtd_Conversion
Male_Cav_Overflow_Yr_4 = (Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal)*Male_4_Yr_Wtd_Conversion
Male_Cav_Overflow_Yr_5 = (Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal)*Male_5_Yr_Wtd_Conversion
Male_Cav_Overflow_Yr_6 = (Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal)*Male_6Yr_Wtd_Conversion
Male_Cav_Overflow__Yr_2 = (Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal)*Male_2_Yr_Wtd_Conversion
Net_OG = (Longleaf_Life_Cycle_End + Longleaf_Old_Growth_Mort +
Longleaf_Old_Growth_Fire_Loss) - Longleaf_Mature_to_Old_Growth
Total_Cavity_Constraint_Dispersal = Logistic_Term-Total_Adult_Male_Death_Rate-
Total_Male_Dispersal
Total_Adults = Total_Adult_Females+Total_Adult_Males
Total_Female_Dispersal = (Total_Adult_Females-RCW__Breeding_Pair)
Total_Male_Dispersal = IF((Total_Adult_Males-
RCW__Breeding_Pair)>(3*RCW__Breeding_Pair))THEN((Total_Adult_Males-
RCW__Breeding_Pair)-(3*RCW__Breeding_Pair))ELSE(0)

```

Graphical relationships:

Diversity_Factor_Adjustment = GRAPH(Diversity_Remaining_%)
(10.0, 0.005), (19.0, 0.1), (28.0, 0.2), (37.0, 0.295), (46.0, 0.4), (55.0, 0.5), (64.0, 0.6),
(73.0, 0.69), (82.0, 0.8), (91.0, 0.895), (100, 1.00)

Foraging_Quality_Index = GRAPH(ForageTrees_per_Bird)
(0.00, 0.00), (1.50, 0.0475), (3.00, 0.0975), (4.50, 0.147), (6.00, 0.198), (7.50, 0.248),
(9.00, 0.297), (10.5, 0.35), (12.0, 0.398), (13.5, 0.448), (15.0, 0.5)

Fitness_Effect_on_Mortality = GRAPH(RCW_Fitness)
(0.00, 1.10), (0.1, 1.09), (0.2, 1.08), (0.3, 1.07), (0.4, 1.06), (0.5, 1.05), (0.6, 1.04), (0.7,
1.03), (0.8, 1.02), (0.9, 1.01), (1, 1.00)

Understory_Encroachment_Index = GRAPH(Hardwood_Understory_Encroachment)
(0.00, 0.5), (15.0, 0.45), (30.0, 0.4), (45.0, 0.348), (60.0, 0.297), (75.0, 0.245), (90.0,
0.198), (105, 0.15), (120, 0.103), (135, 0.05), (150, 0.00)

Hardwood_Fire_Loss_Coeff = GRAPH(Controlled_Fire)
(0.00, 0.00), (150, 9.00), (300, 22.0), (450, 31.5), (600, 40.5), (750, 52.5), (900, 62.5),
(1050, 70.5), (1200, 81.0), (1350, 92.5), (1500, 100)

Hardwood_Mature_Mort_Coeff = GRAPH(Hardwood_Mature_Den)
(0.00, 0.00), (10.0, 0.00), (20.0, 0.03), (30.0, 0.055), (40.0, 0.11), (50.0, 0.155), (60.0,
0.23), (70.0, 0.34), (80.0, 0.463), (90.0, 0.62), (100, 1.00)

Hardwood_Sap_Mort_Coeff = GRAPH(Hardwood_Sapling_Den)
(0.00, 0.00), (60.0, 0.02), (120, 0.045), (180, 0.085), (240, 0.12), (300, 0.16), (360,
0.225), (420, 0.3), (480, 0.42), (540, 0.595), (600, 1.00)

Hardwood_Seed_Survival_Per_Mature_Tree = GRAPH(Hardwood_Sapling_Den)
(0.00, 5.00), (50.0, 3.23), (100, 2.50), (150, 1.68), (200, 1.25), (250, 0.775), (300, 0.525),
(350, 0.175), (400, 0.00), (450, 0.00), (500, 0.00)

Fraction_Sunlight_Penetrated = GRAPH(Longleaf_Tree_Density)
(0.00, 1.00), (100, 0.64), (200, 0.345), (300, 0.195), (400, 0.115), (500, 0.065), (600,
0.03), (700, 0.015), (800, 0.005), (900, 0.005), (1000, 0.00)

Hardwood_Choking_Effect = GRAPH(Hardwood_Density)
(0.00, 0.995), (30.0, 0.97), (60.0, 0.95), (90.0, 0.935), (120, 0.9), (150, 0.835), (180,
0.77), (210, 0.69), (240, 0.59), (270, 0.435), (300, 0.00)

Longleaf_Grass_Fire_Loss_Coeff = GRAPH(Controlled_Fire)
(0.00, 0.00), (700, 0.00), (1400, 0.00), (2100, 0.00), (2800, 0.00), (3500, 0.00), (4200,
0.00), (4900, 0.00), (5600, 2.50), (6300, 13.5), (7000, 100)

Longleaf_Groundcover_Effects = GRAPH(Fuel)
(0.00, 1.00), (2.00, 0.58), (4.00, 0.432), (6.00, 0.348), (8.00, 0.28), (10.0, 0.24), (12.0, 0.212), (14.0, 0.2), (16.0, 0.2), (18.0, 0.2), (20.0, 0.2)

Longleaf_LP_Fire_Loss_Coeff = GRAPH(Controlled_Fire)
(0.00, 0.00), (700, 1.00), (1400, 2.50), (2100, 6.50), (2800, 9.50), (3500, 16.5), (4200, 28.0), (4900, 46.5), (5600, 67.0), (6300, 85.0), (7000, 99.5)

Longleaf_Mature_Fire_Loss_Coeff = GRAPH(Controlled_Fire)
(0.00, 0.00), (700, 0.00), (1400, 1.50), (2100, 2.50), (2800, 5.50), (3500, 8.00), (4200, 14.5), (4900, 28.0), (5600, 48.0), (6300, 66.5), (7000, 100)

Longleaf_Old_Growth_Fire_Loss_Coeff = GRAPH(Controlled_Fire)
(0.00, 0.00), (700, 0.00), (1400, 0.00), (2100, 0.00), (2800, 0.00), (3500, 0.00), (4200, 0.00), (4900, 0.00), (5600, 0.00), (6300, 2.00), (7000, 100)

Longleaf_Sap_Fire_Loss_Coeff = GRAPH(Controlled_Fire)
(0.00, 0.00), (700, 42.0), (1400, 66.0), (2100, 77.0), (2800, 85.5), (3500, 90.5), (4200, 94.5), (4900, 97.5), (5600, 98.5), (6300, 99.0), (7000, 101)

Longleaf_SP_Fire_Loss_Coeff = GRAPH(Controlled_Fire)
(0.00, 0.00), (700, 0.00), (1400, 1.50), (2100, 13.0), (2800, 27.0), (3500, 51.5), (4200, 66.5), (4900, 77.5), (5600, 87.5), (6300, 94.5), (7000, 100)

Fledg_Foraging_Mort_Effect = GRAPH(FCW_Fitness)
(0.00, 1.22), (0.1, 1.20), (0.2, 1.18), (0.3, 1.16), (0.4, 1.13), (0.5, 1.11), (0.6, 1.09), (0.7, 1.07), (0.8, 1.04), (0.9, 1.02), (1, 1.00)

Helper_Effect = GRAPH(Helpers_per_Breeding_Pair)
(0.00, 1.00), (0.2, 1.08), (0.4, 1.15), (0.6, 1.23), (0.8, 1.30), (1.00, 1.39), (1.20, 1.46), (1.40, 1.53), (1.60, 1.60), (1.80, 1.67), (2.00, 1.75)

Appendix B: STELLA Flow Diagrams

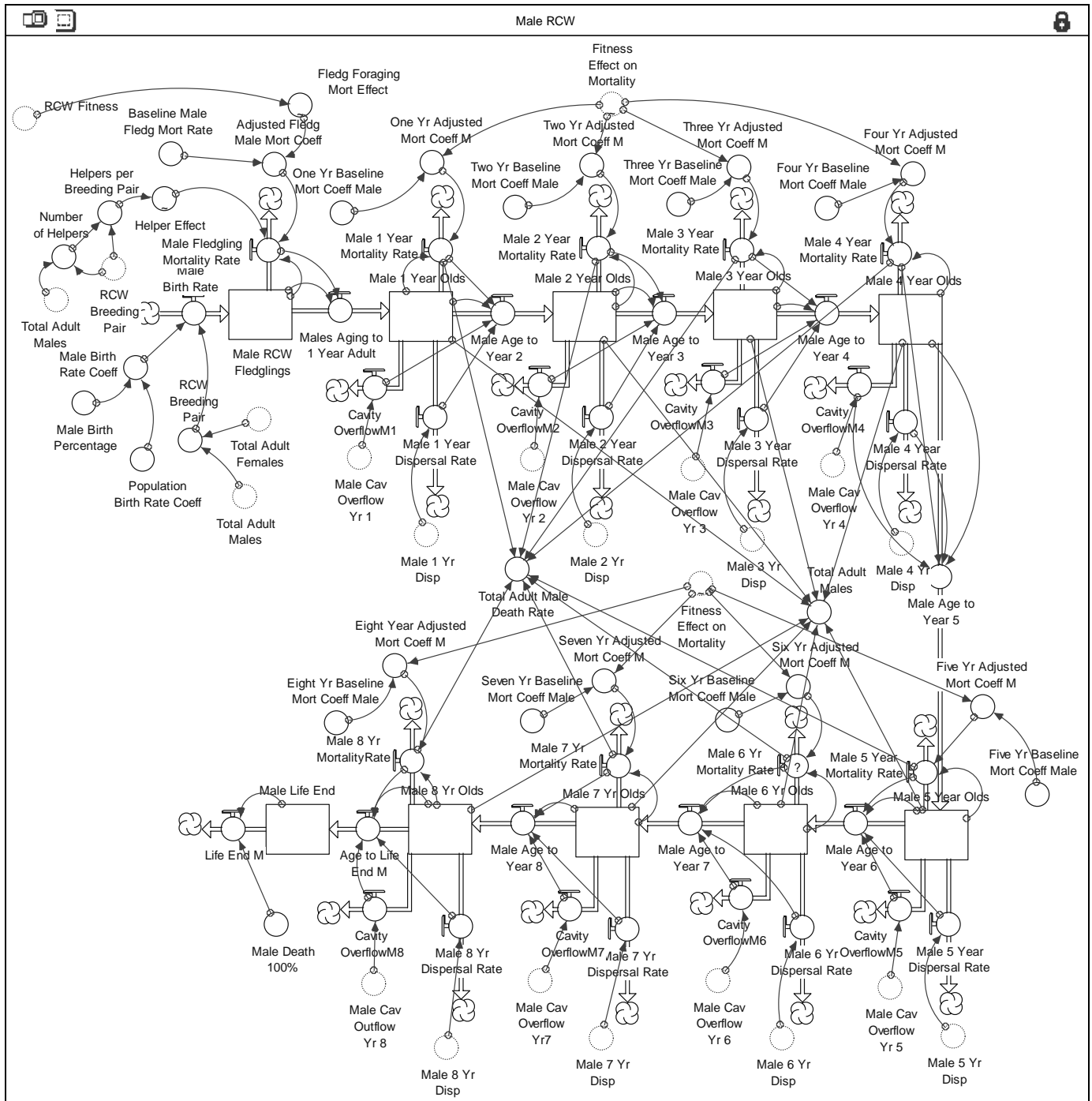


Figure A.1 Male RCW age class flow diagram

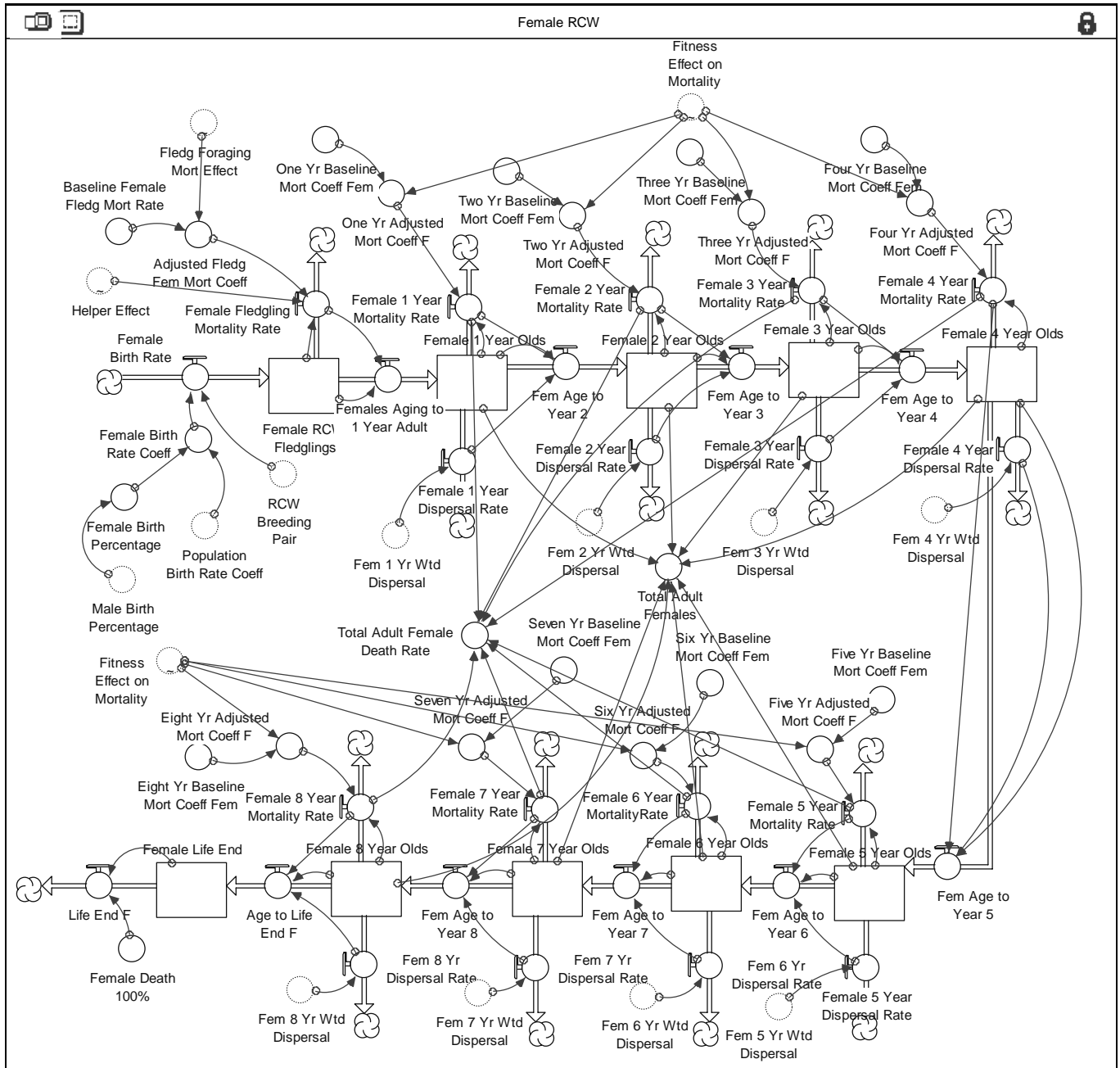
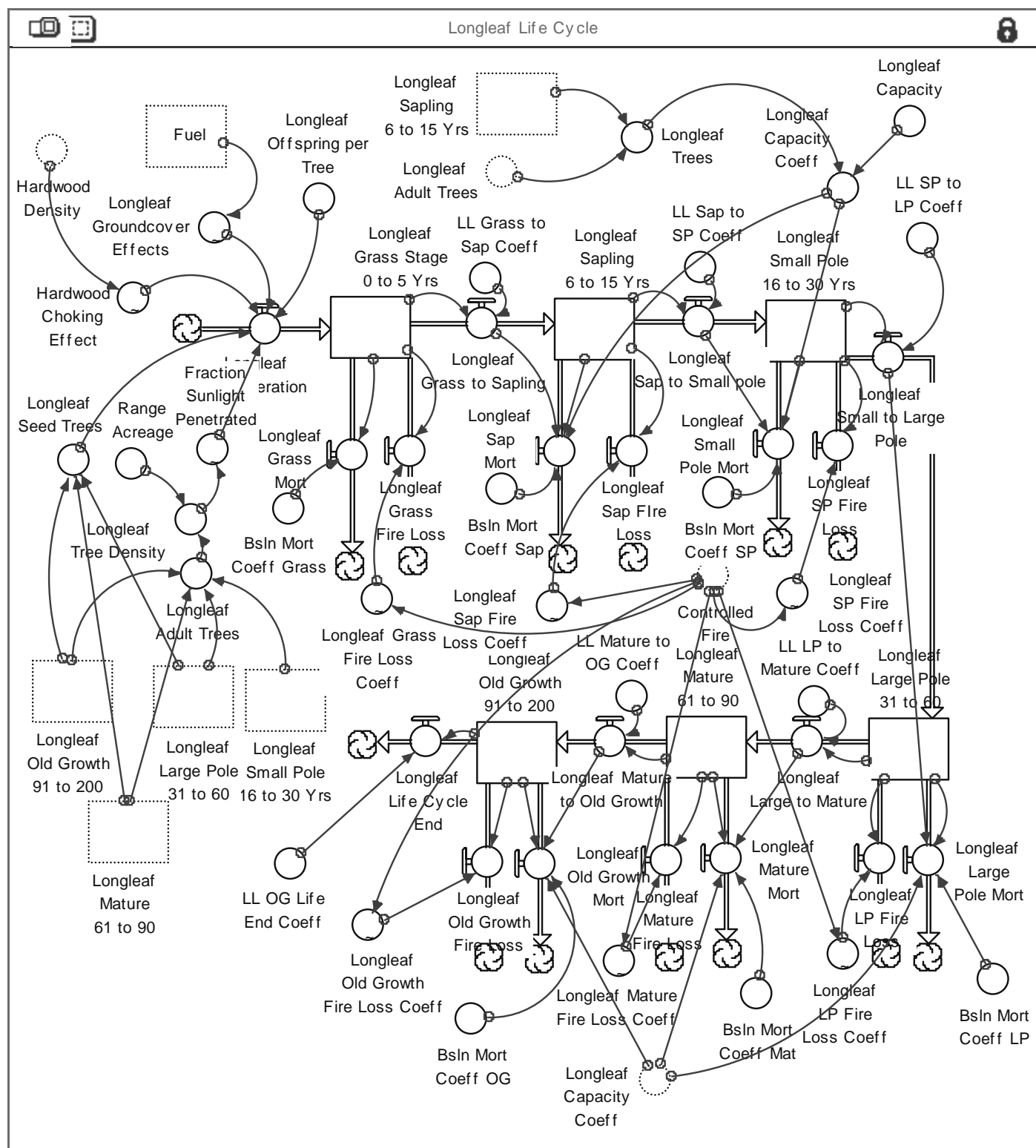
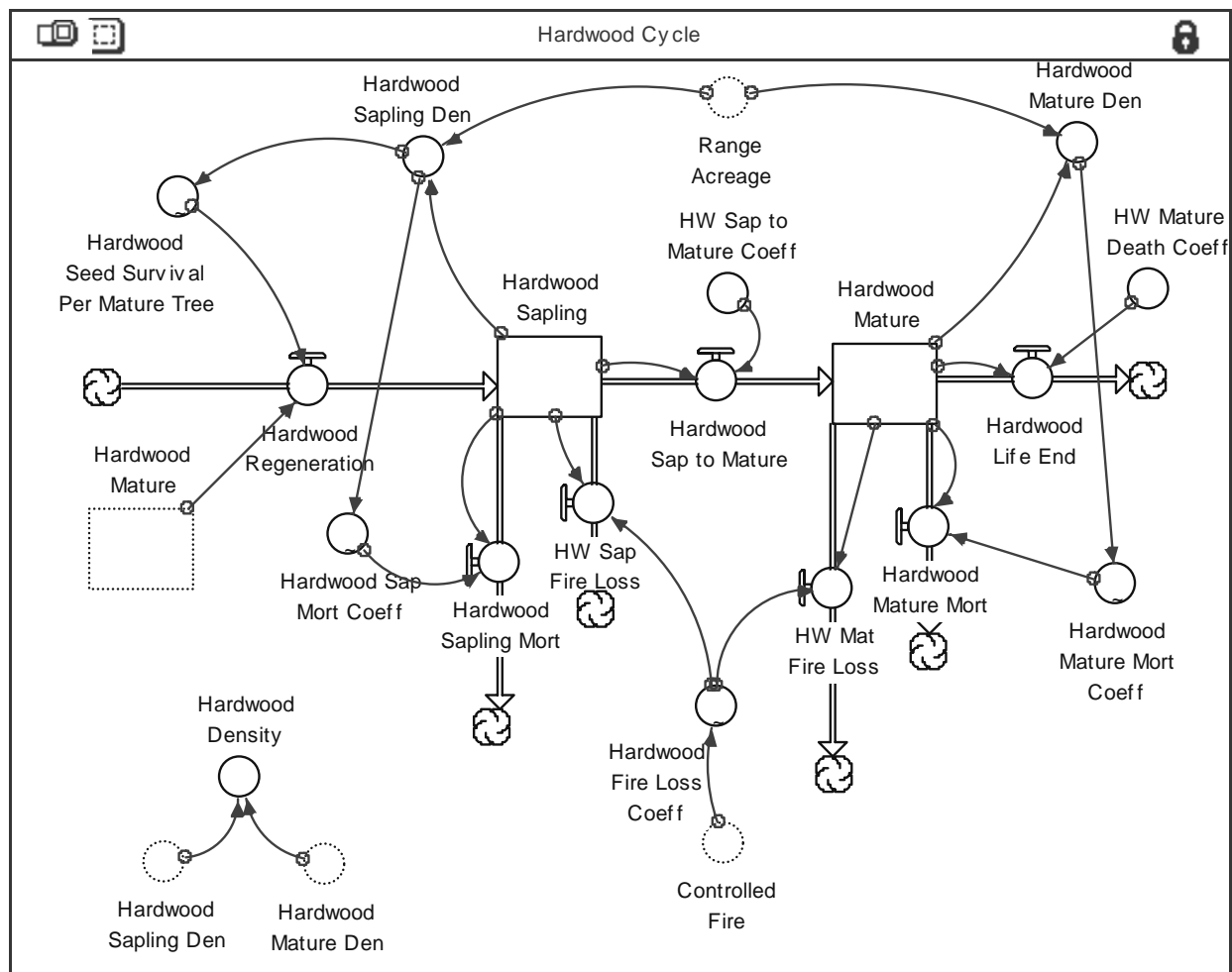


Figure A.2 Female RCW age class flow diagram





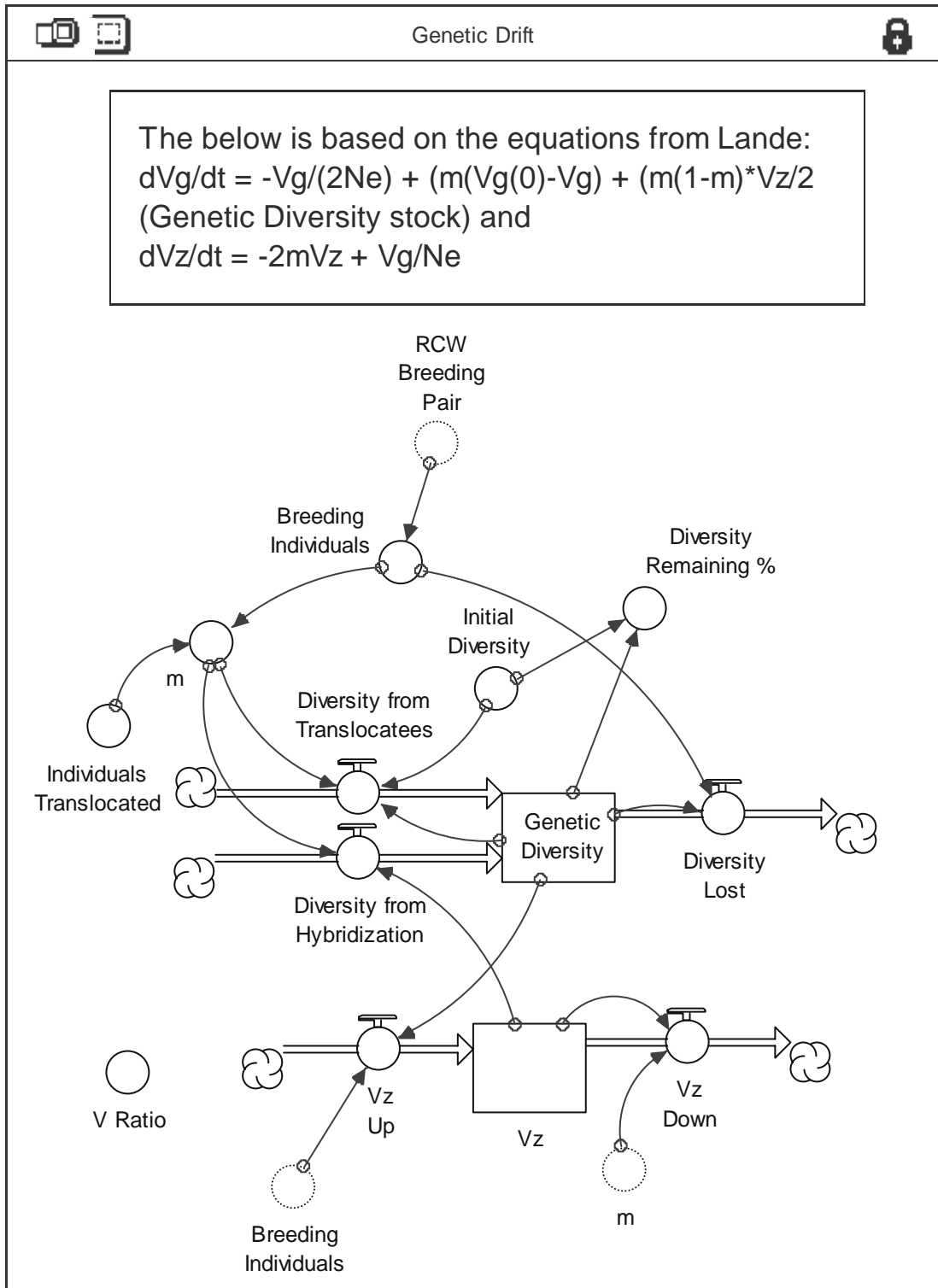


Figure A.4 Genetic diversity flow diagram

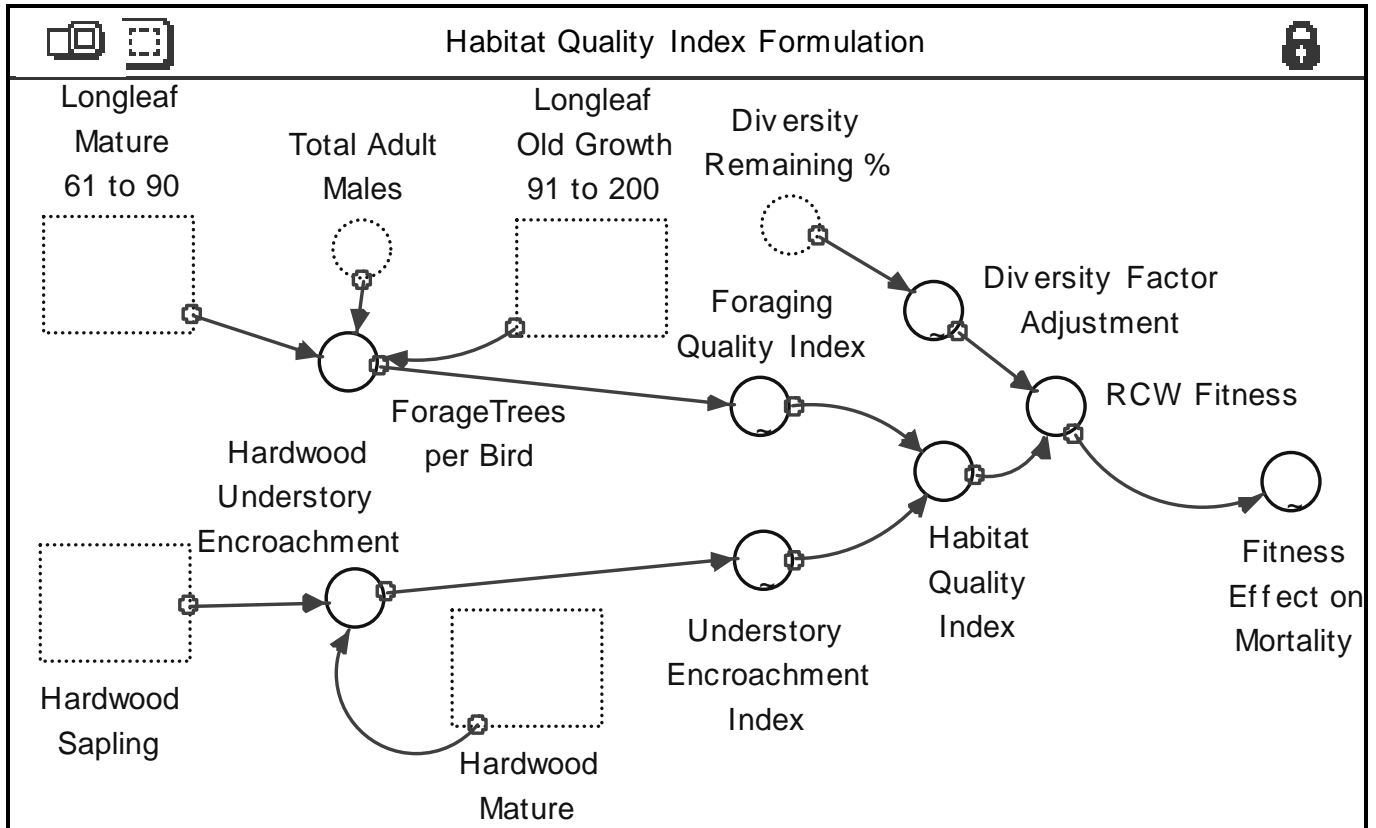


Figure A.5 Habitat Quality Index (HQI) and RCW fitness flow diagram

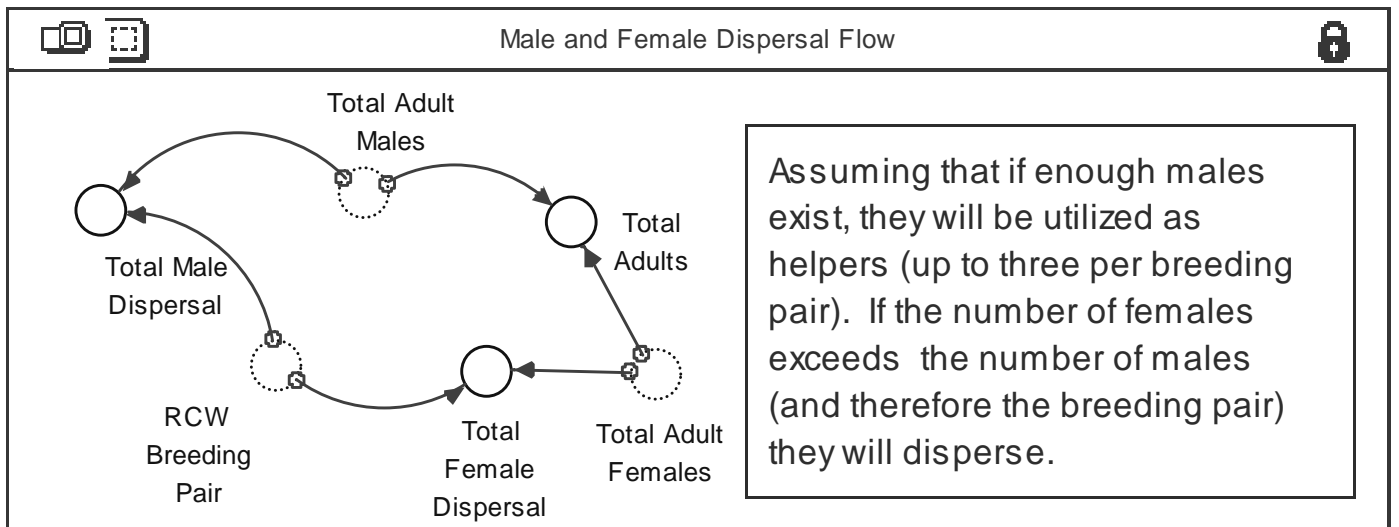


Figure A.6 Male and female RCW dispersal flow diagram

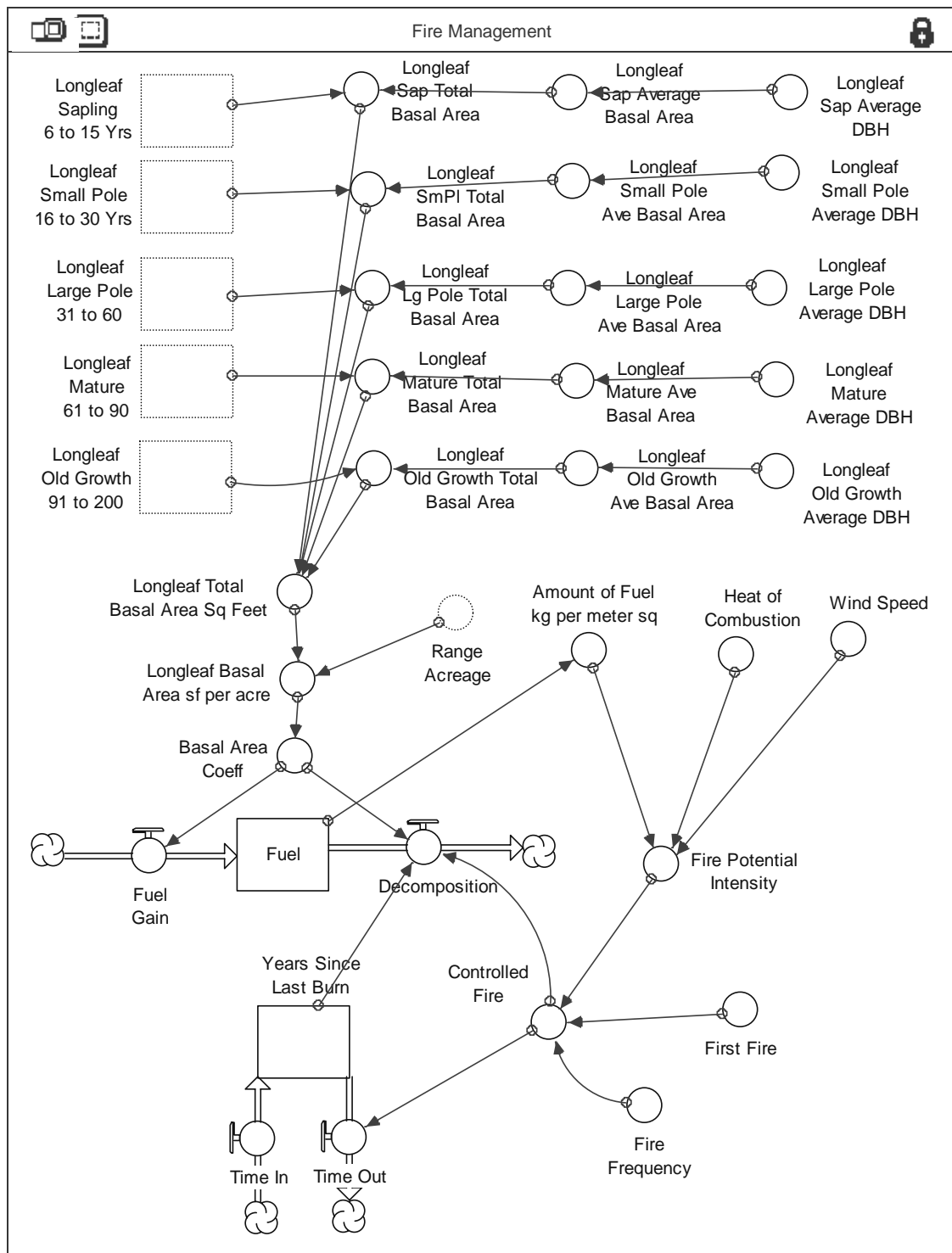


Figure A.6 Longleaf basal area and prescribed burning flow diagram

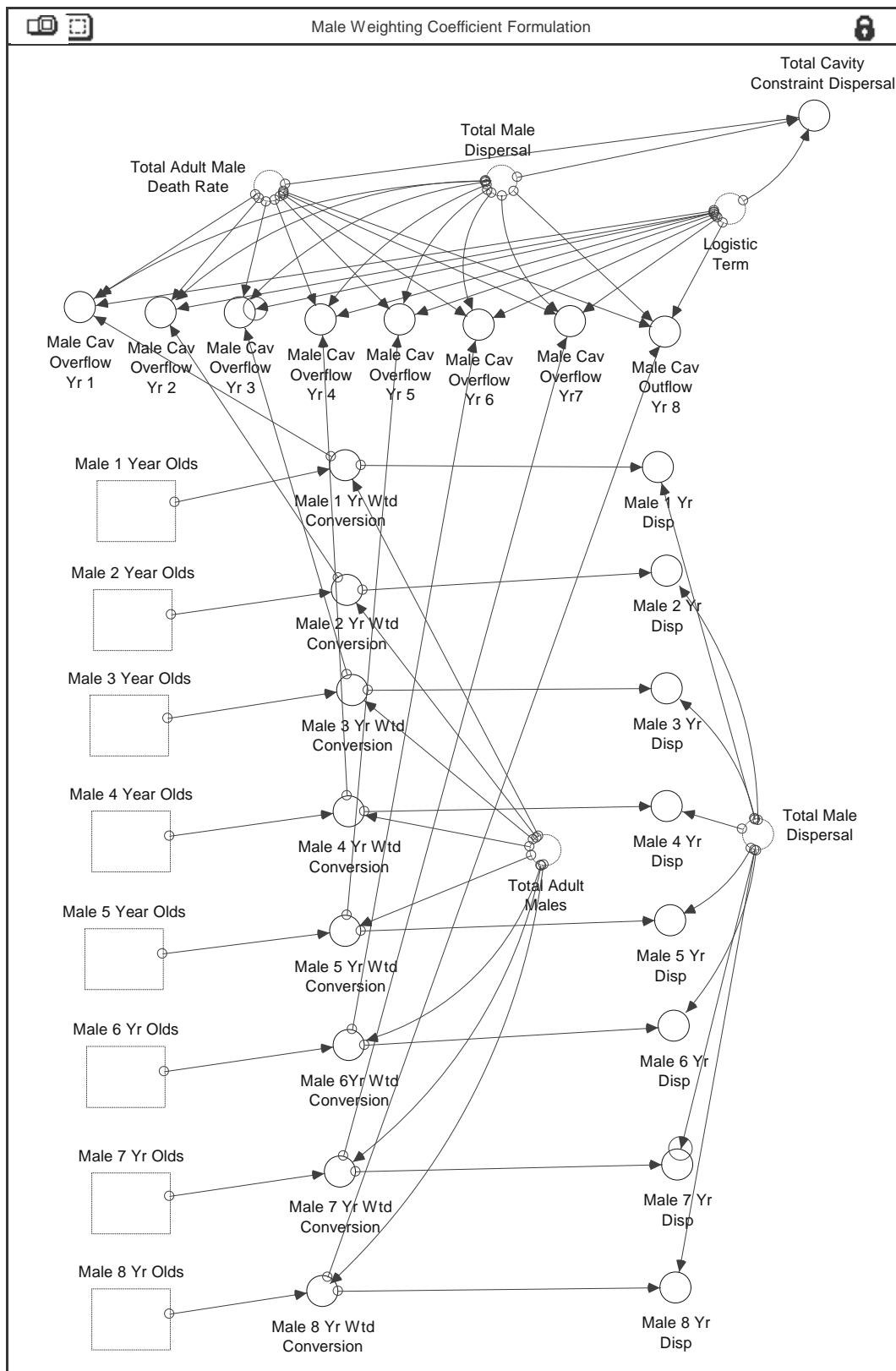


Figure A.7 Male RCW weighted dispersal flow diagram

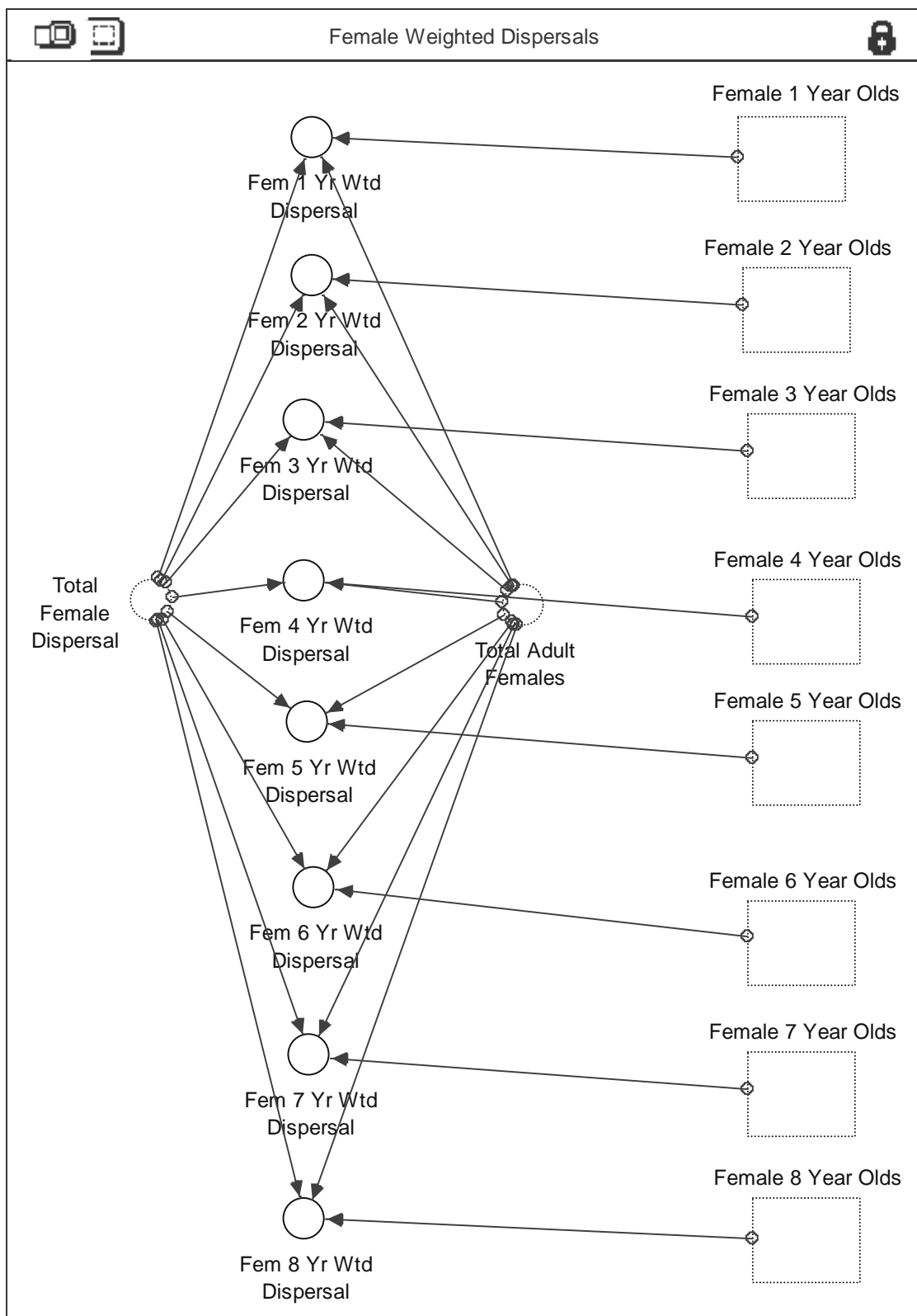


Figure A.8 Female weighted dispersal flow diagram

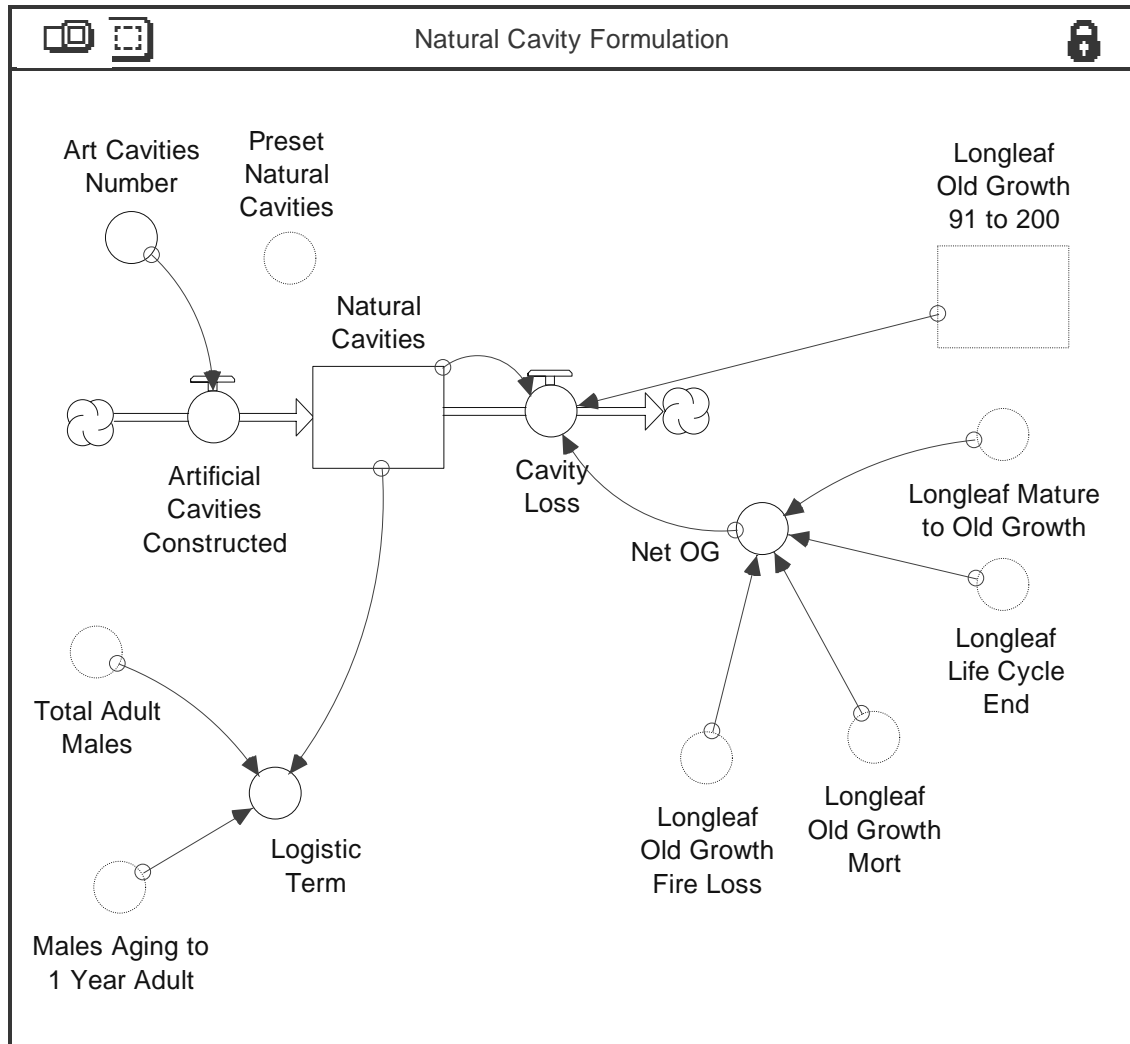


Figure A.9 Natural cavity flow diagram including the logistic term that causes male RCW dispersal due to a lock of vacant cavities

Appendix C: Full Range of Model Output

Run	Trendline Shape	Lower Value	Inputs				# Translocated
			LL Pine Initial State	RCW Initial State	Burn Cycle		
1	Linear	30	Marginal	Average		6	0
2	Umbrella	30	Marginal	A		6	0
3	Bowl	30	Marginal	A		6	0
4	L	10	Marginal	A		6	0
5	L	20	Marginal	A		6	0
6	L	30	Marginal	A		6	0
7	L	40	Marginal	A		6	0
8	L	50	Marginal	A		6	0
9	L	30	Poor	A		6	0
10	L	30	Marginal	A		6	0
11	L	30	Good	A		6	0
12	L	30	Excellent	A		6	0
13	L	30	Marginal	Susceptible		6	0
14	L	30	Marginal	Average		6	0
15	L	30	Marginal	Healthy		6	0

Diversity Remaining	Breeding Pair	Total Adults	Outputs		
			HQI	Old Growth Trees	Mature Trees
69	29	66	0.55	546	662
76	63	143	0.91	546	662
26	3	8	0	546	662
71	36	83	0.65	546	662
71	32	75	0.61	546	662
69	29	66	0.55	546	662
68	24	56	0.45	546	662
65	18	43	0.29	546	662
64	22	50	0.47	535	673
69	29	66	0.55	546	662
73	36	83	0.6	554	651
64	20	47	0.46	512	688
7	2	4	0	546	662
69	29	66	0.55	546	662
81	56	129	0.7	546	662

Run	Trendline Shape	Lower Value	Inputs				# Translocated
			LL Pine Initial State	RCW Initial State	Burn Cycle		
2	L	10	Poor	A		6	0
3	L	10	Poor	H		6	0
4	L	10	Marginal	S		6	0
5	L	10	Marginal	A		6	0
6	L	10	Marginal	H		6	0
7	L	10	Good	S		6	0
8	L	10	Good	A		6	0
9	L	10	Good	H		6	0
10	L	10	Excellent	S		6	0
11	L	10	Excellent	A		6	0
12	L	10	Excellent	H		6	0
13	L	20	Poor	S		6	0
14	L	20	Poor	A		6	0
15	L	20	Poor	H		6	0
16	L	20	Marginal	S		6	0
17	L	20	Marginal	A		6	0
18	L	20	Marginal	H		6	0
19	L	20	Good	S		6	0
20	L	20	Good	A		6	0
21	L	20	Good	H		6	0
22	L	20	Excellent	S		6	0
23	L	20	Excellent	A		6	0
24	L	20	Excellent	H		6	0
25	L	30	Poor	S		6	0
26	L	30	Poor	A		6	0
27	L	30	Poor	H		6	0
28	L	30	Marginal	S		6	0
29	L	30	Marginal	A		6	0
30	L	30	Marginal	H		6	0
31	L	30	Good	S		6	0
32	L	30	Good	A		6	0
33	L	30	Good	H		6	0
34	L	30	Excellent	S		6	0
35	L	30	Excellent	A		6	0
36	L	30	Excellent	H		6	0
37	L	40	Poor	S		6	0
38	L	40	Poor	A		6	0
39	L	40	Poor	H		6	0
40	L	40	Marginal	S		6	0
41	L	40	Marginal	A		6	0
42	L	40	Marginal	H		6	0
43	L	40	Good	S		6	0
44	L	40	Good	A		6	0
45	L	40	Good	H		6	0
46	L	40	Excellent	S		6	0
47	L	40	Excellent	A		6	0
48	L	40	Excellent	H		6	0
49	L	50	Poor	S		6	0
50	L	50	Poor	A		6	0
51	L	50	Poor	H		6	0
52	L	50	Marginal	S		6	0
53	L	50	Marginal	A		6	0
54	L	50	Marginal	H		6	0
55	L	50	Good	S		6	0
56	L	50	Good	A		6	0

Diversity Remaining	Breeding Pair	Total Adults	Outputs		
			HQI	Old Growth Trees	Mature Trees
67	28	64	0.61	535	673
73	39	60	0.67	535	662
15	3	7	0.05	546	662
71	36	83	0.65	546	662
82	62	142	0.77	546	662
15	3	7	0.05	554	651
75	44	101	0.69	554	651
86	72	166	0.75	554	651
15	3	7	0.05	512	688
66	26	60	0.6	512	688
84	65	148	0.77	512	688
10	2	5	0	535	673
66	25	58	0.55	535	673
73	36	83	0.63	535	673
11	2	5	0	546	662
71	32	75	0.61	546	662
82	59	137	0.74	546	0.662
11	2	5	0	554	651
74	40	92	0.65	554	651
86	70	162	0.74	554	651
11	2	5	0	512	688
65	23	54	0.54	512	688
84	63	145	0.76	512	688
7	2	4	0	535	673
64	22	50	0.47	535	673
72	32	74	0.58	535	673
7	2	4	0	546	662
69	29	66	0.55	546	662
81	56	129	0.7	546	662
7	2	4	0	554	651
73	36	83	0.6	554	651
86	68	158	0.73	554	651
7	2	4	0	512	688
64	20	47	0.46	512	688
84	61	140	0.74	512	688
4	1	3	0	535	673
62	17	41	0.35	535	673
71	27	64	0.49	535	673
4	1	3	0	546	662
68	24	56	0.45	546	662
81	51	118	0.65	546	662
4	1	3	0	554	651
72	31	72	0.52	554	651
85	66	151	0.7	554	651
4	1	3	0	512	688
61	17	39	0.34	512	688
83	57	132	0.69	512	688
2	1	2	0	535	673
58	13	30	0.16	535	673
68	22	51	0.36	535	673
2	1	2	0	546	662
65	18	43	0.29	546	662
80	45	106	0.58	546	662
2	1	2	0	554	651
70	25	58	0.39	554	651

Run	Trendline Shape	Lower Value	Inputs				# Translocated
			LL Pine Initial State	RCW Initial State	Burn Cycle		
57	L	50	Good	H		6	0
58	L	50	Excellent	S		6	0
59	L	50	Excellent	A		6	0
60	L	50	Excellent	H		6	0
61	U	10	Poor	S		6	0
62	U	10	Poor	A		6	0
63	U	10	Poor	H		6	0
64	U	10	Marginal	S		6	0
65	U	10	Marginal	A		6	0
66	U	10	Marginal	H		6	0
67	U	10	Good	S		6	0
68	U	10	Good	A		6	0
69	U	10	Good	H		6	0
70	U	10	Excellent	S		6	0
71	U	10	Excellent	A		6	0
72	U	10	Excellent	H		6	0
73	U	20	Poor	S		6	0
74	U	20	Poor	A		6	0
75	U	20	Poor	H		6	0
76	U	20	Marginal	S		6	0
77	U	20	Marginal	A		6	0
78	U	20	Marginal	H		6	0
79	U	20	Good	S		6	0
80	U	20	Good	A		6	0
81	U	20	Good	H		6	0
82	U	20	Excellent	S		6	0
83	U	20	Excellent	A		6	0
84	U	20	Excellent	H		6	0
85	U	30	Poor	S		6	0
86	U	30	Poor	A		6	0
87	U	30	Poor	H		6	0
88	U	30	Marginal	S		6	0
89	U	30	Marginal	A		6	0
90	U	30	Marginal	H		6	0
91	U	30	Good	S		6	0
92	U	30	Good	A		6	0
93	U	30	Good	H		6	0
94	U	30	Excellent	S		6	0
95	U	30	Excellent	A		6	0
96	U	30	Excellent	H		6	0
97	U	40	Poor	S		6	0
98	U	40	Poor	A		6	0
99	U	40	Poor	H		6	0
100	U	40	Marginal	S		6	0
101	U	40	Marginal	A		6	0
102	U	40	Marginal	H		6	0
103	U	40	Good	S		6	0
104	U	40	Good	A		6	0
105	U	40	Good	H		6	0
106	U	40	Excellent	S		6	0
107	U	40	Excellent	A		6	0
108	U	40	Excellent	H		6	0
109	U	50	Poor	S		6	0
110	U	50	Poor	A		6	0
111	U	50	Poor	H		6	0
112	U	50	Marginal	S		6	0
113	U	50	Marginal	A		6	0
114	U	50	Marginal	H		6	0
115	U	50	Good	S		6	0
116	U	50	Good	A		6	0
117	U	50	Good	H		6	0
118	U	50	Excellent	S		6	0
119	U	50	Excellent	A		6	0
120	U	50	Excellent	H		6	0
121	B	10	Poor	S		6	0
122	B	10	Poor	A		6	0
123	B	10	Poor	H		6	0
124	B	10	Marginal	S		6	0
125	B	10	Marginal	A		6	0
126	B	10	Marginal	H		6	0
127	B	10	Good	S		6	0
128	B	10	Good	A		6	0
129	B	10	Good	H		6	0
130	B	10	Excellent	S		6	0
131	B	10	Excellent	A		6	0
132	B	10	Excellent	H		6	0

Diversity Remaining	Breeding Pair	Total Adults	Outputs			Old Growth Trees	Mature Trees
			HQI				
85	62	143	0.67			554	651
2	1	2	0			512	688
58	12	29	0.15			512	688
83	52	121	0.63			512	688
40	18	41	0.84			535	673
72	55	126	0.93			535	673
77	65	149	0.91			535	673
40	18	41	0.84			546	662
76	65	147	0.92			546	662
83	75	171	0.86			546	662
40	18	41	0.84			554	651
78	69	158	0.89			554	651
87	84	192	0.82			554	651
40	18	41	0.84			512	688
72	51	116	0.93			512	688
85	76	174	0.85			512	688
40	17	39	0.79			535	673
72	55	125	0.92			535	673
77	65	148	0.91			535	673
40	17	39	0.79			546	662
76	64	146	0.92			546	662
83	74	170	0.86			546	662
40	17	39	0.79			554	651
78	69	157	0.89			554	651
87	83	191	0.82			554	651
40	17	39	0.79			512	688
71	50	115	0.92			512	688
85	76	173	0.85			512	688
39	14	33	0.62			535	673
72	54	123	0.91			535	673
77	64	147	0.91			535	673
39	14	33	0.63			546	662
76	63	144	0.92			546	662
83	74	170	0.86			546	662
39	14	33	0.63			554	651
78	68	156	0.88			554	651
86	83	190	0.82			554	651
39	14	33	0.63			512	688
71	50	113	0.91			512	688
85	75	172	0.89			512	688
34	7	18	0			535	673
72	52	120	0.9			535	673
77	63	145	0.91			535	673
35	7	18	0			546	662
75	62	142	0.91			546	662
83	74	169	0.88			546	662
35	7	18	0			554	651
78	68	155	0.88			554	651
86	83	190	0.82			554	651
35	7	18	0			512	688
71	48	110	0.89			512	688
85	75	172	0.85			512	688
23	4	9	0			535	673
72	50	115	0.88			535	673
77	62	141	0.9			535	673
23	4	9	0			546	662
75	60	137	0.89			546	662
83	73	167	0.85			546	662
23	4	9	0			554	651
78	67	152	0.87			554	651
86	82	188	0.81			554	651
23	4	9	0			512	688
71	47	106	0.87			512	688
85	74	171	0.84			512	688
0	1	1	0			535	673
26	3	8	0.03			535	673
42	5	12	0.05			535	673
0	1	1	0			546	662
33	4	10	0.04			546	662
68	13	32	0.12			546	662
0	1	1	0			554	651
42	5	12	0.05			554	651
79	25	60	0.2			554	651
0	1	1	0			512	688
28	3	8	0.03			512	688
75	19	45	0.17			512	688

Inputs							Outputs					
Run	Trendline Shape	Lower Value	LL Pine Initial State	RCW Initial State	Burn Cycle	# Translocated	Diversity Remaining	Breeding Pair	Total Adults	HQI	Old Growth Trees	Mature Trees
133	B	20	Poor	S	6	0	0	1	1	0	535	673
134	B	20	Poor	A	6	0	23	3	7	0.01	535	673
135	B	20	Poor	H	6	0	39	5	11	0.03	535	673
136	B	20	Marginal	S	6	0	0	1	1	0	546	662
137	B	20	Marginal	A	6	0	30	4	9	0.02	546	662
138	B	20	Marginal	H	6	0	66	12	28	0.09	546	662
139	B	20	Good	S	6	0	0	1	1	0	554	651
140	B	20	Good	A	6	0	38	5	11	0.03	554	651
141	B	20	Good	H	6	0	87	83	191	0.82	554	651
142	B	20	Excellent	S	6	0	0	1	1	0	512	688
143	B	20	Excellent	A	6	0	26	3	8	0.01	512	688
144	B	20	Excellent	H	6	0	74	17	41	0.14	512	688
145	B	30	Poor	S	6	0	0	0	1	0	535	673
146	B	30	Poor	A	6	0	20	3	6	0	535	673
147	B	30	Poor	H	6	0	36	4	10	0.01	535	673
148	B	30	Marginal	S	6	0	0	0	1	0	546	662
149	B	30	Marginal	A	6	0	27	3	8	0	546	662
150	B	30	Marginal	H	6	0	63	10	25	0.07	546	662
151	B	30	Good	S	6	0	0	0	1	0	554	651
152	B	30	Good	A	6	0	35	4	10	0.01	554	651
153	B	30	Good	H	6	0	77	20	48	0.13	554	651
154	B	30	Excellent	S	6	0	0	0	1	0	512	673
155	B	30	Excellent	A	6	0	23	3	7	0	512	688
156	B	30	Excellent	H	6	0	72	15	37	0.1	512	688
157	B	40	Poor	S	6	0	0	0	1	0	535	673
158	B	40	Poor	A	6	0	17	2	6	0	535	673
159	B	40	Poor	H	6	0	32	4	9	0	535	673
160	B	40	Marginal	S	6	0	0	0	1	0	546	662
161	B	40	Marginal	A	6	0	23	3	7	0	546	662
162	B	40	Marginal	H	6	0	61	9	22	0.05	546	662
163	B	40	Good	S	6	0	0	0	1	0	554	651
164	B	40	Good	A	6	0	30	4	8	0	554	651
165	B	40	Good	H	6	0	75	17	42	0.09	554	651
166	B	40	Excellent	S	6	0	0	0	1	0	512	688
167	B	40	Excellent	A	6	0	21	3	6	0	512	688
168	B	40	Excellent	H	6	0	71	13	32	0.07	512	688
169	B	50	Poor	S	6	0	0	0	1	0	535	673
170	B	50	Poor	A	6	0	14	2	5	0	535	673
171	B	50	Poor	H	6	0	28	3	8	0	535	673
172	B	50	Marginal	S	6	0	0	0	1	0	546	662
173	B	50	Marginal	A	6	0	20	2	6	0	546	662
174	B	50	Marginal	H	6	0	57	8	19	0.02	554	651
175	B	50	Good	S	6	0	0	0	1	0	554	651
176	B	50	Good	A	6	0	26	3	7	0	554	651
177	B	50	Good	H	6	0	73	15	36	0.07	554	651
178	B	50	Excellent	S	6	0	0	0	1	0	512	688
179	B	50	Excellent	A	6	0	18	2	6	0	512	688
180	B	50	Excellent	H	6	0	68	12	28	0.05	512	688

**Figure C.1 Full range of model output (simulations 1-180).
The first 15 simulations shown make up the sensitivity analysis**

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Vita

Captain Ryan E. Nelson graduated from Ozark High School in Ozark, Arkansas. He entered undergraduate studies at the University of Arkansas in Fayetteville, Arkansas where he graduated with a Bachelor of Science degree in Biological and Agricultural Engineering in May 2001. He was commissioned as a second lieutenant through AFROTC Detachment 030 at the University of Arkansas.

His first assignment was to the 14th Civil Engineer Squadron, Columbus AFB, Mississippi, in May 2001. While stationed at Columbus AFB, Captain Nelson was the Natural Resources Manager. His responsibilities included managing the forestry and wildlife programs on approximately 5000 acres of federal land. His efforts brought the first ever prescribed burn program into effect on Columbus AFB, a program that is still in use at Columbus AFB. He also revamped the base wildlife conservation policy and was a major contributor to the writing of the Integrated Natural Resources Management Plan at Columbus AFB. At the end of his assignment, Capt Nelson's efforts won the Department of Defense Natural Resources Conservation Award (small base) for 14th Civil Engineer Squadron Environmental Flight at Columbus AFB.

In August 2004, he entered the Graduate School of Engineering and Management, Air Force Institute of Technology. Upon graduation, he will be assigned to the 314th Civil Engineering Squadron, Little Rock AFB, Arkansas.

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4. TITLE AND SUBTITLE An Exploration of the Effects of Genetic Drift on the Endangered Red-Cockaded Woodpecker				5a. CONTRACT NUMBER		
				5b. GRANT NUMBER		
				5c. PROGRAM ELEMENT NUMBER		
				5d. PROJECT NUMBER		
6. AUTHOR(S) Nelson, Ryan E., Captain, USAF				5e. TASK NUMBER		
				5f. WORK UNIT NUMBER		
7. PERFORMING ORGANIZATION NAMES(S) AND ADDRESS(S) Air Force Institute of Technology Graduate School of Engineering and Management (AFIT/EN) 2950 Hobson Way WPAFB OH 45433-7765				8. PERFORMING ORGANIZATION REPORT NUMBER AFIT/GEM/ENV/06M-12		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES) n/a				10. SPONSOR/MONITOR'S ACRONYM(S)		
				11. SPONSOR/MONITOR'S REPORT NUMBER(S)		
12. DISTRIBUTION/AVAILABILITY STATEMENT APPROVED FOR PUBLIC RELEASE; DISTRIBUTION UNLIMITED.						
13. SUPPLEMENTARY NOTES						
14. ABSTRACT The Red-cockaded Woodpecker (RCW) (<i>Picoides borealis</i>) is classified as an endangered species under the Endangered Species Act of 1973 due to habitat fragmentation and prescribed burn suppression. Given the endangerment of the RCW, the genetic variation of the small populations will decrease over time due to random genetic drift. The only method of battling the negative effects of random genetic drift is to move, or translocate, genetically diverse birds into the fragmented populations thereby increasing the genetic diversity of the small populations. The objective of this research effort was to explore the effects of random genetic drift on small RCW populations, place bounds on those effects, and finally determine the most efficient management strategies to be used in different situations. A model, representing the RCW and their longleaf ecosystem, is simulated over 75 years (75 RCW generations) and the management practices are monitored for up to 300 years. A study of the model results shows that ecosystem managers need to rethink their methods of managing endangered populations. Instead of focusing on the quality of the physical habitat using land management techniques, the model suggests that when the population low in numbers, translocation is the only management technique capable of restoring the endangered population.						
15. SUBJECT TERMS Red-cockaded Woodpecker, Genetic Drift, Genetic Modeling, Endangered Species, Translocation, Land Management						
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT		18. NUMBER OF PAGES	
a. REPOR T	b. ABSTR ACT	c. THIS PAGE	UU		129	
U	U	U			19a. NAME OF RESPONSIBLE PERSON Michael L. Shelley, Ph.D. (ENV) 19b. TELEPHONE NUMBER (Include area code) (937) 255-3636, ext 7287	

Standard Form 298 (Rev. 8-98)
 Prescribed by ANSI Std. Z39-18

	Form Approved OMB No. 074-0188
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